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BIOLOGY OF RUST RESISTANCE IN FOREST TREES:

PROCEEDINGS OF A NATO-IUFRO ADVANCED STUDY INSTITUTE AUGUST 17-24, 1969



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DEPARTMENT OF AGRICULTURE

MISCELLANEOUS PUBLICATION NO. 1221
FEBRUARY 1972

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PROCEEDINGS OF A NATO-IUFRO ADVANCED STUDY INSTITUTE

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This NATO-IUFRO Advanced Study Institute, Basic Biology and International Aspects of Rust Resistance in Forest Trees, was supported by the North Atlantic Treaty Organization; the International Union of Forestry Research Organizations; the Forest Service, U. S. Department of Agriculture; and the University of Idaho.

The Institute was held at the University of Idaho, Moscow, Idaho, U.S.A.

RICHARD T. BINGHAM, SCIENTIFIC DIRECTOR

RAYMOND J. HOFF AND GERAL I. MCDONALD, PROGRAM COORDINATORS

MISCELLANEOUS PUBLICATION NO. 1221

U.S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D.C.

FOREST SERVICE
FEBRUARY 1972

Library of Congress Catalog Card Number: 71-180872

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington, D. C. 20402 - Price $4.
Stock Number 0100-2425

PREFACE

A message from George M. Jemison, President, IUFRO, states--

"Around the world today is a steadily growing pressure on forest resources--pressure to produce the many goods and services that such lands provide. Highly developed countries and those striving for greater social and economic gains, both look to forests for the material wealth and environment to satisfy human needs.

"But as efforts increase to manipulate natural forests to better serve mankind, we find that many new problems arise and old ones intensify. Forestry scientists have responded by bringing their skills to focus more effectively on a large array of critical problems.

"Forest geneticists and pathologists have sought for a long time to comprehend, to utilize, and to stabilize genetic resistance to rust diseases of forest trees. Rust diseases are known to be a major cause of huge timber losses in many parts of the world. Faced with substantial gaps in knowledge and problem solutions of great technical difficulty, the small band of dedicated forest biologists has made steady progress in understanding the biology of rust resistance in forest trees."

Amplifying the comments of Dr. Jemison, the significance of these problems is illustrated by the fact that in the U.S.A. two tree rusts, one introduced and one indigenous, in a single year accounted for losses of pine growing stock and sawtimber equivalent to 375 million cubic feet of wood.[1] And in Europe, a glacially impoverished pine flora is sustaining increasing rust losses in the altered environments of forest plantations, while substitution of promising pine introductions often is stymied either by indigenous or introduced rusts.

Two very challenging problems face biologists concerned with tree rust resistance. These biologists are forced to proceed with more than the usual quota of ignorance. Nearly complete voids exist in their knowledge of sexuality and pathogenic variability in the tree rusts, and in their knowledge of the mechanisms and genetics of host resistance. Second, economic hosts for which they seek resistance are perennial, long-lived gymno- or angiosperms. Reproductive cycles in these trees may range from 5 to 25 or more years while the rust may be cycling 10 to more than 100 times.

Hopefully the small band of biologists can expect greater public support for attacking these problems, now that crowded humanity is more vociferously demanding increased productivity of clean air and water, of recreational and aesthetic opportunity, and of wood, fiber, fuel and other

[1] *U. S. Dep. Agr., Forest Service. 1958. Timber resources for America's future. Forest Resource Rept. 14. 713 p. (bd. ft. data converted using 7 bd. ft. = 1 cu. ft.).*

forest products from diminishing forest lands. Certainly it is most timely to seek biologically sound and ecologically safe ways to prevent forest tree losses that both mar the landscape and lower productivity of the world's forests. Genetic resistance is one means of pest control with all of the required specifications.

It was in this hopeful atmosphere that the timeliness of an international symposium on the biology of rust resistance in forest trees was perceived. Originally the idea was restricted to white pine blister rust resistance. Thus the present proceedings contains 15 papers assaying the world's white pines--their intrinsic qualities, relative blister rust resistance and international exchange. However, after establishment of the International Union of Forestry Research Organizations (IUFRO), Subject Group on Genetic Resistance to Forest Diseases and Insects--in 1967--organizers were encouraged to broaden symposium coverage to forest tree rust resistance in general.

Forest biologists of the U.S. Forest Service, and of many other federal and state forestry services, forestry colleges, and private forestry agencies from around the world attended the Advanced Study Institute and contributed to these proceedings. Their interest, concern, and deep involvement in the problem of increasing the world's supply of wood through development of biologically-safe controls for forest pests is reflected in that attendance, and in the quality of the papers assembled in these proceedings. They are recommended to all biologists who share this concern.

ACKNOWLEDGMENTS

The Scientific Director and Program Coordinators for the Advanced Study Institute owe many thanks to many persons. Welcome help was received from NATO, IFURO, the USDA Forest Service, and the University of Idaho. The good services of individuals in these organizations were greatly appreciated and made a significant contribution to the success of the conference.

Programing, field trips, travel, and many other arrangements were handled by staff of the Forestry Sciences Laboratory, USDA Forest Service, Moscow, Idaho, and of the St. Joe National Forest, Northern Region. Financial support for the Institute came from NATO's Scientific Division and was most capably administered by Division Director H. Arnth-Jensen. Vital scientific support from the international forestry community was offered by IUFRO President George M. Jemison and by Henry D. Gerhold, Leader of IUFRO's Subject Group for Genetic Resistance to Forest Diseases and Insects. Facilities of the University of Idaho were provided by President Ernest W. Hartung and Dean Ernest Wohletz of the College of Forestry, Range, and Wildlife Sciences.

RICHARD T. BINGHAM,
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THE GENETICS OF RUST FUNGI

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ABSTRACT

Genetic studies of rusts depend on a thorough understanding and manipulation of their life cycles. The two rusts we know most about genetically, stem rust (*Puccinia graminis tritici*) and flax rust (*Melampsora lini*), differ principally in that the former infects two host genera, wheat and barberry, while the latter infects only flax. In both cases the economically important phase is the dikaryon which is clonally multiplied on an enormous scale by uredospores. In white pine blister rust (*Cronartium ribicola*) perennial haploid homokaryotic infections are important on the economic host, white pine, but are not multiplied by a spore form. In the past control has been based largely on eradication of the alternate host, *Ribes*, which harbors the dikaryon. Breeding white pine for resistance is thus directed against the haploid meiotic products of the rust (basidiospores), a situation closely analagous to breeding apples for resistance to scab (*Venturia*). We may expect that genetic variation among white pine infections is likely to be maximal unless reduction of the alternate host population is severe enough to promote inbreeding of the rust.

Until now the obligate parasitism of the rusts has limited spontaneous and induced markers to those which affect host range and morphology. With these markers sexual and parasexual genetic systems have been established as well as cytoplasmic inheritance. In addition to growth chamber, greenhouse and field studies on the host, genetic analysis can make use of electron microscopy, serology, recovery of intact mycelium from the host plant, and more recently, culture on synthetic media.

There seems little reason to doubt that the chief features of other genetically better known fungi apply also to the rusts. At the present time this assumption offers little by way of directly suggesting new control measures. What it does mean, however, is that our understanding of the mechanisms of inhibition, antagonism, enzyme regulation and repression and other aspects of fungal metabolism may well give a "spin-off" in the form of improved fungicides and more sophisticated ways of evaluating host resistance.

The opportunities for genetic studies in any organism are dictated by such aspects of its biology as life cycle, generation time, experimental convenience and, increasingly nowadays, its economic significance. In all respects except the last, the rusts present obstacles. But their destructive effects on man's food and fiber crops far outweigh the other considerations and rusts have in fact been the subject of more intensive genetic study than any other group of fungal pathogens. This paper does not review the considerable literature on rust genetics but is rather an introduction to the basic features of theory and practice with some discussion of recent work and some speculation about the future of rust genetics.

RUST LIFE CYCLES

In common with other basidiomycetes rusts have two phases, a homokaryon made up of haploid uninucleate cells and a dikaryon made up of binucleate cells. The dikaryon in some respects is equivalent to a diploid since in each cell of the mycelium the same two nuclei are present. Five well defined stages, denoted 0 - IV, characterize the development of the most complex or "long-cycle" rusts.

0. PYCNIA (SPERMOGONIA) AND SPERMATIA (PYCNIOSPORES)

The flask-shaped pycnia develop as a result of infection by a haploid basidiospore. In the cavity of the pycnium, uninucleate spermatia are formed which act as fertilizing elements. They are carried in the drop of sugary fluid which exudes from the opening of the pycnium. Receptive hyphae produced by the pycnium extend into the drop of fluid. Here they fuse only with compatible spermatia from a different pycnium carried there by insects or rain splashes. Fusion between spermatia and receptive hyphae is governed by a simple bipolar heterothallism. The two mating types are denoted + and -. Spermatia are unable to initiate new infections so this phase of the rust, although it may grow perennially, is unable to repeat itself by spore dispersal. Clonal propagation can be achieved by transfer of infected tissue in laboratory studies (Hermansen, 1959; Garrett, 1960; Patton, 1962).

I. AECIA AND AECIOSPORES

These are produced as a result of the sexual fusion described above. The nuclei of the spermatia migrate through the hyphae of the pycnium, passing from cell to cell through the septal pores until they reach an aecial rudiment. The resulting dikaryon produces an aecium or pustule consisting of chains of binucleate aeciospores which eventually burst through the host epidermis. The aeciospores are released usually by a discharge mechanism and may infect an appropriate host.

II. UREDIA AND UREDOSPORES

The uredia result from infection by aeciospores or uredospores. The infecting mycelium is a dikaryon and the uredospores are stalked binucleate cells. When released they can repeat this cycle of infection for as long as conditions remain favorable.

III. TELIA AND TELEUTOSPORES

Teleutospores are binucleate cells produced in groups (telia) following infection by aeciospores or uredospores. They are not released but germinate while still attached to the host material or debris. In some rusts germination follows overwintering; in others, such as *Cronartium ribicola*[1] teliospores germinate in the season they are formed.

IV. BASIDIOSPORES

Before the teleutospore germinates, its two genetically different haploid nuclei fuse. This diploid nucleus moves into the germ tube and undergoes meiosis. Three cross walls form which cut off the four haploid meiotic products. Each cell forms one basidiospore (sporidium) which is discharged at maturity. The germ tube, or promycelium, is thus a basidium.

In the heteroecious rusts, such as *C. ribicola* or *Puccinia graminis*, pycnia and aecia are produced on one host, uredia and telia on another quite unrelated host. In autoecious rusts, such as *Melampsora lini*, all phases occur on one host species. In some short cycle rusts, such as *P. malvacearum*, only telial and basidiospore phases occur. Such rusts are presumably homothallic and the pycnial-aecial mechanism promoting outbreeding is dispensed with. Other so-called "imperfect rusts" are only known in aecial and uredial stages and are referred to form-genera.

Some special points concerning *C. ribicola* on white pine should be noted here. Pycnia appear on the bark of adjacent stems or branches some 24 to 26 months after needle infection. The aecia appear among the pycnial scars one year later. Thus from stage 0 to I takes at least 3 years. In spite of these difficulties, Hirt (1964) carried out a detailed study of pycnial and aecial development which indicates that transfer of nectar between pycnia is not necessary for aecial development. Unfortunately single spore inoculation could not be made to establish whether or not aecia will arise from single basidiospore infections. Prior to aeciospore production, cell fusions occur in the developing aecium. Dikaryotic cells are formed which then bud off chains of aeciospores. Aecia frequently arise between pycnia, suggesting that they could well be of hybrid or mixed origin even if *Cronartium* is homothallic.

GENETIC MARKERS

In any genetic study heritable differences are needed. To date the obligate parasitism of the rusts has meant that only characters revealed during growth on the host plant can be used. However, the discovery that certain strains of *P. graminis tritici* can be cultured on artificial media opens up other possibilities.

VIRULENCE

The most commonly used markers are those affecting virulence. We may define virulence as the pathogen property of producing severe disease symptoms on a host variety carrying major gene resistance. Virulence, and its alternative avirulence, toward members of a set of differential host varieties provides us with the means of classifying rust isolates into

[1] *Authorities for Latin binomials are given in the subject index.*

physiologic races. The gene-for-gene hypothesis developed by Flor (1956a), and discussed by Loegering (these proceedings) provides a rational genetic scheme for explaining this interrelationship. The practical importance of rust resistance and the problems created by physiologic specialization explains why so much attention has been paid to genetic studies of virulence. The nature of host resistance and hence the nature of pathogen avirulence and virulence are of course relevant to this discussion and are briefly considered later.

The availability of virulence markers depends on the availability of differentially resistant strains of the economic host. Unless physiologic specialization has been detected virulence markers will not normally be available. But this does not mean that they cannot be induced. Many studies with rusts have shown that virulent mutants may be isolated spontaneously or following treatment with a mutagen (Table 1). Presumably, if treated spores were applied to a susceptible host, mutants with reduced virulence could be detected and, if their fitness were not too greatly impaired, could be propagated and used as markers. Indeed such forms were observed in crosses between certain races of *M. lini* (Flor, 1950) and as a result of inbreeding *P. graminis tritici* (Johnson and Newton, 1938). Both examples illustrate how selection works against such mutants arising in nature.

In the heteroecious rusts, one would expect to find resistance in both hosts and indeed this is so. Race 15B of *P. graminis* is unable to infect barberry by basidiospores (Green and Johnson, 1958). D'Oliveira (1940) has shown variation in susceptibility to basidiospore infection by *P. triticina* among species of *Thalictrum*, by *P. anomala* among species of *Ornithogalum* and by *P. coronata* among species of *Rhamnus*. We may also note the resistance of *Ribes usuriense*, and the variety Consort derived from it by hybridization with *R. nigrum* (Hunter and Davis, 1943), to infection by aeciospores and uredospores of *C. ribicola*.

In autoecious rusts like *M. lini* where all the spore forms occur on flax, the virulence markers which determine the host range of the dikaryon also function in the haploid infection. Avirulence in *M. lini* is dominant in the dikaryon (Flor, 1965). Haploid pycnia on a resistant host necessarily carry the appropriate allele(s) for virulence. If their receptive hyphae are fertilized with spermatia carrying a dominant allele for avirulence, produced on a susceptible host, we may ask whether aecia and aeciospores will form on the resistant host. In fact, aeciospores are formed even though they are unable to infect the host genotype which bore them (Flor, 1959). A comparable experiment with pigment mutants of *P. graminis* on barberry is noted below.

While in some circumstances the gene-for-gene relationship largely determines the outcome of rust-host interactions we must not lose sight of the fact that pathogen fitness and adaptability is subject to many other controls which may not be so susceptible to genetic analysis. We call this variation in aggressiveness and assume that it is determined, like non-race specific or "field" resistance in the host, by polygenes.

The two aspects of pathogenicity, virulence and aggressiveness, have been considered in some detail by van der Plank (1968) in relation to the problem of disease resistance and are also dealt with by Zadoks (these proceedings) in his paper.

Table 1. Spontaneous and induced mutants in rusts

Species	Spontaneous[a]	Induced	Agent
Virulence			
Melampsora lini		Flor, 1956b	U.V.
		Schwinghammer, 1959	Fast neutrons, X-ray, U.V.
		Flor, 1960b	X-ray
Puccinia coronata avenae	Zimmer *et al.*, 1963	Griffiths & Carr, 1961	U.V.
P. graminis tritici	Stakeman *et al.*, 1930		
	Newton & Johnson, 1939		
	Watson, 1957a		
	Watson & Luig, 1968	Rowell *et al.*, 1963	X-ray
P. recondita	Samborski, 1963		
P. striiformis	Gassner & Straib, 1932	Stubbs, 1968	?
	Macer, 1967		
Spore color			
M. lini (Smooth wall)	Flor, 1965[b]		
P. graminis avenae	Johnson, 1949[b]	Baker & Teo, 1966[b]	EMS
P. graminis secalis	Green, 1964[b,c]		
P. graminis tritici	Newton & Johnson, 1927[b,c]	Luig, 1967[b]	EMS
	Cotter, 1934[c]		
	Joshi & Kak, 1955[b]		
	Misra & Lele, 1955[b]		
	Bridgmon, 1959[b]		
	Garret & Line, 1962[b,c]		
	Watson & Luig, 1962a[b]		
	Green, 1964[b,c]		
	Luig, 1967[b]		
P. helianthi	Brown, 1940[b,c]		
P. hordei	Luig & Baker, 1956[b]		
P. triticina	Brown & Johnson, 1949[b]		

[a] see also Johnson, 1946 [b] = uredial stage; [c] = pycnia and aecia

MORPHOLOGICAL MARKERS

The most commonly used morphological markers are those with altered spore pigmentation. The cytoplasm of the uredospores of *P. graminis* normally contains an orange carotenoid pigment. The uredospore wall is brown. The two colors superimposed produce the normal reddish brown color of wild type uredospores. Newton and Johnson (1927) described two spontaneous pigment mutants: "orange" was due to colorless wall and "grayish-brown" was due to colorless cytoplasm. Both characters were recessive (Newton, Johnson, and Brown, 1930). Selfing an F_1 between the two mutants revealed a third or double mutant class with white spores in the F_2. These spores had colorless walls and cytoplasm.

Some other white mutants of *P. graminis tritici* and *P. graminis secalis* examined by Green (1964) behaved in a similar way. These white mutants were observed by inoculating barberry with basidiospores produced by telia collected in the field. Normal pycnial lesions are orange; the mutant pycnia were white. The white pycnia were rather infertile and the color of the few aecia which developed after fertilization depended on the source of the fertilizing spermatia. If these came from white pycnia, white aecia were formed. If the spermatia came from normal orange pycnia, then orange aecia formed showing that "white", or colorless cytoplasm, was recessive. White aecial spores from material presumed to be *P. graminis secalis* gave no infections on wheat, rye, or oats. White aeciospores of *P. graminis tritici* showed poor ability to infect wheat but the uredia that were established from white aecia were grayish-brown in color.

In *P. graminis*, Watson and Luig (1962b) found many mutations to colorless wall and noted that all common Australian strains of stem rust are available as orange uredospore stock cultures as well as wild type. Baker and Teo (1966) treated uredospores of *P. graminis avenae* with the chemical mutagen, ethyl methane sulphonate (EMS). They recovered yellow, orange, and gray-brown mutants. The yellow mutant was reported as lacking color in the uredospore wall but whether it was a double mutant or a wall color mutant with a pleiotropic effect on the carotenoid of the cytoplasm was not determined.

In the same experiments Baker and Teo recovered two mutants in which development of teleutospores was accelerated. At a day temperature of 27°C, uredospores of these mutants inoculated to susceptible oat seedlings immediately gave rise to telia. Uredia were only formed at lower temperatures. Wild type strains do not form telia on leaves of greenhouse grown plants and in the field telia are restricted to mature plant stems. Mutants of this kind could present certain genetic advantages.

Apart from the lowered infectivity or avirulence of the white mutants noted above, no gross changes in pathogenicity are associated with the pigment mutants although the tests applied were not very sensitive. Anthraquinone pigment mutants of the tomato leaf mould disease fungus *Cladosporium fulvum* show a marked disadvantage in competition with the parent, wild-type strain which, however, is not so marked as the disadvantage imposed by possessing unnecessary genes for virulence (Day, 1968).

Other morphological mutants in rusts are uncommon. The stringent selection imposed by obligate parasitism presumably eliminates those mutants which might be useful in genetic studies but which have the effect of lowering fitness or reducing aggressiveness. Even so Flor (1965) has recorded a recessive uredospore mutant with a smooth wall rather than the

rough wall of wild type. The mutant was observed in a greenhouse culture because the spores appeared redder than wild type and remained clumped together. The latter property would no doubt lead to its rapid elimination in the field.

MUTATION IN THE DIKARYON

Genetic studies with *Neurospora* and other laboratory fungi are greatly helped by the ready availability of haploid cells and mycelium. Recessive mutants appear directly in homokaryons which survive treatment with mutagens and a variety of procedures are available for screening specific classes of mutants (Fincham and Day, 1965). The difficulties of screening for mutants in dikaryotic or diploid microorganisms are well known (Snow, 1966). In higher plants the screening procedure is carried out on individuals which are raised following self-pollination of the treated generation. Recessive mutants are recovered as homozygotes. In the pathogen *Phytophthora infestans*, lack of success in obtaining auxotrophic or virulence mutants, which in other fungi are generally recessive, has been used as evidence for diploidy (McKee, 1969; Clark and Robertson, 1966).

To date all induced mutation studies in rusts have been directed at treating uredospores. These dikaryotic spores are of course functionally equivalent to diploids. Two approaches have been made. The first is to irradiate uredospores from cultures known to be heterozygous for certain recessive virulence markers and to screen for mutants in which the recessive virulence is revealed (Flor, 1956b; Schwinghamer, 1959; Rowell, Loegering, and Powers, 1963). With X-rays or neutrons, the most frequent class of mutants to be expected are chromosomal deletions which include the dominant avirulence allele. An analysis of two such X-ray induced mutants of *M. lini* by Flor (1960b) tends to confirm such an explanation but raises many more questions about the nature of virulence than it answers (Day, 1966).

The second method is to treat the uredospores of a clone of undetermined genotype and screen for virulent mutants on one or several different hosts resistant to the parent clone. A mutant recovered from *P. coronata avenae* by Griffiths and Carr (1961) following U.V. treatment of uredospores was virulent on 6 oat varieties, all with different factors for resistance to which the parent race was avirulent. The mutant was also avirulent to a seventh variety to which the parent was virulent. It seems likely that one result of U.V. irradiation was to induce genetic recombination to generate the mutant. This is more plausible than the induction of 7 separate but simultaneous mutations.

An approach which does not appear to have been tried is the treatment of teleutospores either just prior to or during germination (meiosis) with screening for mutants among the infections produced by the basidiospores formed by the treated material. Green's (1964) search for pigment mutants of *P. graminis* was essentially by this method but without mutagen treatment. The mutants Green recovered were probably present as heterozygotes since their frequency was quite high in those teleutospore collections where they occurred. Presumably this method could be used to isolate induced mutants of *C. ribicola* on *Pinus*. An important advantage of screening haploid spores is that recovery of recessive markers is much more efficient. However, in most rusts it is difficult to obtain consistent teleutospore formation, germination, and high rates of infection with

basidiospores. Mutants like those found by Baker and Teo (1966) in *P. graminis avenae* could well be useful.

Screening for mutants among meiotic products of basidiomycetes in general has received rather little attention. I tried unsuccessfully to recover white or pale basidiospore mutants of *Coprinus lagopus* by X-ray treatment of immature fruit bodies (Day, unpublished).

The recovery of recessive mutants from treated dikaryons raises the question of how they arise. Unless the genetic constitution of the dikaryon is known, induced homozygosity of recessive markers by mitotic crossing over will confound the picture. For virulence markers the question is complicated by the fact that we know little about the nature of virulence itself. To illustrate my point: avirulence may be the result of a pathogen substance (in this instance a specific inducer) interacting with the host to initiate a response which we will call "resistance". Is virulence merely the lack of such an inducer? If so, then a small deletion which removes the gene specifying the inducer, providing it is not lethal, would be expected to produce a virulent phenotype. The recognition and identification of small deletions requires a considerable amount of background knowledge which is not available in the rusts. Even in *Venturia inaequalis* where some 19 different loci controlling virulence have been identified and, in many cases, mapped (Bagga and Boone, 1968) we cannot say whether virulence is recessive to avirulence at any of these loci, let alone study their interactions, because heterokaryons and diploids of *Venturia* have not been synthesized. Some answers may come, however, from pseudo-wilds if they are stable for long enough. These are cultures which are disomic for one or more chromosomes usually carrying complementary auxotrophic markers. It would be interesting to compare induced virulent mutants in *V. inaequalis* with naturally occurring alleles but no such induced mutants are available.

In experiments where pigment mutants were recovered following treatment of rust uredospores with a mutagen (see Table 1), there is no information on the genotypes of the treated clones so we cannot distinguish between recombination and mutation. Recessive mutants will be recovered from a homozygous dominant dikaryon if both dominant alleles mutate simultaneously, if one mutates and the other is lost in a deletion, or if recombination follows mutation of one of the alleles even though they were presumed to be in separate nuclei at the time of treatment.

MEIOTIC RECOMBINATION

The sexual stage of a long-cycle rust is obtained by germinating teleutospores and infecting the appropriate host with the resultant basidiospores. In order to work with single pycnia this must be done in such a way that scattered or isolated pycnia arise, the majority of which are derived from single basidiospores. Flor (1942), in working with basidiospore infections of *M. lini*, discarded flax leaves with several pycnia and also allowed 4 to 6 days after pycnia appeared for aecia to develop from undetected multiple infections with compatible basidiospores. Spermatia were transferred from one pycnium to another with a wire loop. In flax rust the aecia form 2 to 5 days later but only 50% of the matings are compatible. Where pycnial infections are long lived or can be clonally reproduced, as in *C. ribicola* (Patton, 1962), it should be possible to identify the mating type of parental clones, if indeed they are heterothallic (Hirt, 1964). The aeciospores are used to inoculate a susceptible host to obtain a uredospore clone which can be tested further.

If the nectar drops of two different pycnia are mixed, and aecia result from both, the two aecial progenies stem from reciprocal crosses. The cytoplasmic contributions of spermatia to the aecial rudiment and resultant dikaryon are likely to be very small. Differences between aeciospores from reciprocal crosses will probably be due to cytoplasmic inheritance. In this way cytoplasmic inheritance of virulence was demonstrated by Johnson (1946, 1954) in crosses between different races of *P. graminis tritici*.

Tests for homo- or heterozygosity of different loci are carried out by selfing. This involves transfer of nectar among pycnia produced by basidiospores derived from one dikaryotic clone. In such tests, Flor was careful to make separate transfers between different individual pycnia, maintaining the identity of their aecial progenies. Miah (1968) has discussed the relative merits of this method and others in which spermatia of different pycnial drops are pooled and applied back to the same donor pycnia. In the second method the progenies are derived either from aecia or single aeciospores or from uredia or single uredospores, produced by pooling the aeciospores. Sources of error include mixed pycnia which arise from infection by two or more basidiospores of the same mating type, cross-contamination of aeciospores, and the occurrence of multiple fertilization of single aecial rudiments (Dinoor, Khair, and Fleischmann, 1968a). Multiple infections may have a variety of effects on lesion phenotype, some of which were described by Dinoor *et al.* (1968b) for *P. coronata avenae*. Although tedious, single spore inoculations overcome most of these problems.

In the cereal rusts, the use of benzimidazole solutions (Person, Samborski, and Forsyth, 1957) on which inoculated, detached leaves may be floated in petri dishes has meant that rust free greenhouses, although desirable, are no longer so important. Hooker and Yarwood (1966) cultured *P. sorghi* through all stages on detached leaves of *Oxalis corniculata* and *Zea mays*, proceeding from uredospores to recombinant aeciospores in 5 to 6 weeks at any time of the year.

Genetic analysis of blister rust on white pine would involve haploid phenotypes generated by crossing two different haploid infections. Each basidiospore could only be conveniently tested once because clonal propagation is not easy. Even so, it might be possible to find out if crosses between rusts on two genetically different resistant hosts generate basidiospores able to infect either host or the hybrid incorporating both resistances. If foresters use vertical resistance to blister rust in breeding white pines, then almost certainly such a demonstration will be possible in the future. Some studies demonstrating meiotic recombination in rusts are listed in Table 2.

MITOTIC RECOMBINATION

The fact that rusts vary in the absence of meiotic recombination and the discovery of the parasexual cycle in *Aspergillus* prompted several workers to look for heterokaryosis and parasexuality. Mixing uredospores of two different rust clones is expected to generate two recombinant dikaryons through exchange of partner nuclei, provided hyphal anastomosis takes place. In fact such experiments do generate recombinants but often many more than the two classes expected. For example Watson (1957b) and Watson and Luig (1958) mixed red-spored race 111 with orange-spored race NR-2 of *P. graminis tritici*. The orange race was virulent on 4 wheat

Table 2. Genetic recombination in the rusts

Species	Meiotic recombination[a]	Mitotic recombination
Melampsora lini	Flor, 1956a	Flor, 1957, 1960a, 1964
Puccinia anomala [*P. hordei*]	d'Oliviera, 1939	
P. carthami	McCain, 1959	
P. coronata avenae	Zimmer *et al.*, 1965 Dinoor *et al.*, 1968a	Bartos *et al.*, 1967
P. graminis avenae	Johnson, 1949 Green, 1965 Green & McKenzie, 1967	
P. graminis secalis	Watson & Luig, 1962a Green, 1964	Bridgmon & Wilcoxson, 1959
P. graminis tritici	Wilcoxson & Paharia, 1958 Luig & Watson, 1961 Loegering & Powers, 1962 Kao & Knott, 1969	Nelson *et al.*, 1955 Nelson, 1956 Watson, 1957b Bridgmon, 1959 Ellingboe, 1961 Watson & Luig, 1958 Watson & Luig, 1962b
P. helianthi	Brown, 1936 Craigie, 1959	
P. recondita	Vakili & Caldwell, 1957	Barr *et al.*, 1964
P. sorghi	Flangas & Dickson, 1961 Hooker and Yarwood, 1966	
P. striiformis		Little & Manners, 1967
P. triticina	Brown & Johnson, 1949	

[a]See also Johnson, 1946.

varieties to which the red race was avirulent. Only cultures from red uredia on these 4 wheats were analyzed. Eleven different races stable on further subculturing were found among 100 uredia tested. The information on the genetic control of virulence to certain of the wheat varieties so obtained agreed with information from selfing red-race 111 (Wilcoxson and Paharia, 1958).

The generally accepted explanation for the appearance of this range of classes is that, during growth on the selective host, nuclear fusion and chromosomal reassortment occur to produce recombinant nuclei and hence recombinant dikaryons. The observations of Dinoor *et al.* (1968b) on the range of phenotypes produced by multiple infections illustrates the importance of showing that recombinant phenotypes are in fact stable. This is best done by single spore culturing. The appearance of such recombinants during the vegetative growth of an isolated heterozygous dikaryon could well explain much of what we have called spontaneous mutation. In the rusts we can say little or nothing about the mechanism of meiotic or mitotic recombination but there is little reason to doubt that it is similar to *Ustilago maydis* and other fungi in which crossing over and gene conversion can be recognized (Holliday, 1968). While recombination in diploids (of *Ustilago maydis* or *Saccharomyces cereviseae*) is now much better understood, less attention has been paid to this in dikaryons. Among the scarce published information on this subject are some intriguing results of Ellingboe (1963) in the hymenomycete *Schizophyllum commune* suggestive of genetic transfer of specific loci between separate nuclei. Several examples of mitotic recombinations are noted in Table 2.

The case of *P. striiformis* (Little and Manners, 1967) is of special interest because no pycnial or aecial stages are known for this rust. In this example the recombinant classes could be accounted for by reassortment of intact nuclei.

We should also note that recombination occurs between the varieties of *Puccinia graminis* adapted to different cereals both by sexual hybridization (Johnson, 1946) and by mitotic recombination (Bridgmon and Wilcoxson, 1959). There seems to be no evidence in rusts of heterokaryon incompatibility systems like those found primarily in the ascomycetes and fungi imperfecti which restrict heterokaryons to strains having a common genetic background.

DISCUSSION

While technical difficulties have impeded genetic analysis of rusts and linkage maps, biochemical genetics, and quantitative genetics have still to be developed, the future holds many promises. The discovery that certain Australian strains of *P. graminis tritici* can be cultured on artificial media as dikaryons (Williams *et al.*, 1966, 1967) opens the way to work with induced auxotrophic mutants. These would be especially useful if haploid mycelium can be cultured which, as far as I know, has not yet been determined.

Cultures also afford a much more convenient means of examining the physiology of the rust organism away from its host. At the present time mycelia are only available as spore germlings or fractionated by filtration and density gradient centrifugation, from macerated host tissue (Dekhuijzen, Singh, and Staples, 1967).

The increasing study of rust ultrastructure should also tell us more about the nature of virulent and avirulent (or susceptible and resistant) associations and give us greater insight into a variety of rust phenotypes (reviewed in Day, 1966).

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FLOOR DISCUSSION

PERSON: You suggested that the basis for aggressiveness of the rust may be polygenes, numerous genes with small effects. Would you expand on this a tiny bit?

DAY: The genetic control of fitness or aggressiveness is likely to be much the same as that of stature, vigor, weight and other characters of this kind in higher organisms. They are the culmination of many different processes in the organism. The effects of single genes are detectable but generally you would expect continuous variation among genetically different individuals in a population.

PERSON: Would you suggest that the counterpart to aggressiveness in the host in terms of resistance is field resistance?

DAY: Yes.

PERSON: That's the point I was interested in.

KINLOCH: I have a question for Dr. Day. Would you expect the potential for new virulent races of white pine blister rust to be comparable to that in the cereal rusts? Since we are concerned with a haploid stage which is a product of meiosis and has undergone genetic recombination there is less potential for an explosive buildup of uniform genotypes such as you have in a uredospore population of wheat rust. I would like to bring up another point. If resistance depends on several things, then presumably there are several resistance genes in a host. The pathogen has to have virulence genes to combat them. If it has to go through meiosis there is a chance of an appropriate virulent combination arising in many cases. In forestry we are not worried about harvesting the entire crop. We can afford some susceptibility. If we have good genetic resistance in part of the population and let the pathogen take its toll in the other part what does this imply in terms of selection pressure on the pathogen to generate new races virulent on the resistant portion of the crop. I am thinking of van der Plank's hypothesis that the most fit races are usually those with the fewest necessary genes for virulence. These will tend to propagate themselves as long as there are some suscepts in the population and selection pressure is not too extreme against them.

DAY: In reply to your first question, it seems to me there is no overriding reason for assuming that *Cronartium* is much different from other pathogens in its potential for producing new virulent races. The dikaryotic aecio- and uredospore stages on *Ribes* store variation and you might imagine on that host there would be little or no direct selection for factors controlling aggressiveness on white pine. You can compare *Cronartium* with the smuts, where host infection follows meiosis and there is no clonal reproduction of adapted genotypes, or with apple scab, where although clonal reproduction occurs, tree infection begins anew each spring with haploid meiotic products. There seem to be no barriers to the development of virulent forms in these fungi. I would agree that their development and spread has not been as explosive as in the cereal rusts. Now, I don't know how my reply affects your subsequent questions. Perhaps someone else would care to comment.

PERSON: I believe that the second and third parts of your question will come up more appropriately after we have heard from Dr. Zadoks.

LIMITATIONS AND ADVANTAGES OF CONIFERS, VS. AGRONOMIC CROPS, AS RESISTANCE BREEDING MATERIALS

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ABSTRACT

The space and time extension of trees, the biology of conifers, and the nature of forestry are discussed in relation to the strategy and tactics of breeding for blister rust resistance. The virtual immortality of tree genotypes, achievable by cloning, the longevity and abundance of conifer seed and pollen, and the relative ease of maintaining the identity of large trees are seen as advantages offsetting, in part, the disadvantages of long breeding and test cycles. These features, plus ecotypic diversity and an hypothesis regarding the history of relations between white pines and blister rust are used to support an argument for basing white pine breeding strategies on a very large gene pool.

This title, thoughtfully suggested by our Director, sounds like one of those riddles that starts: "What's the difference between...?" In fact the title leads into one facet of the larger question, "What are the differences between forestry and agriculture?" Unless one is expert in both agriculture and forestry, he is likely to produce answers based on misapprehension of at least one of these activities. I can modestly claim that my ignorance of agriculture is much more extensive than the non-stocked areas of my knowledge of forestry. Therefore I will talk mostly about conifers and very little about agronomic crops.

Most of the tree-breeders in the audience are accustomed to a certain attitude toward their vocation held by the breeders of annual and other ephemeral and unimpressive plants. The attitude appears to be a compound of incredulity, sympathy, and perhaps a tinge of the kind of bewildered admiration we feel for lion-tamers, astronauts, submariners, and university presidents. As I analyze the grounds for this attitude, they seem to consist of the special features of trees in general, of conifers in particular, and of forestry. Moreover, white pine forests and forestry have special features worth noting. I hope to dispel some of the incredulity of our earth-bound colleagues, inform their sympathy, and sustain whatever admiration they may feel.

The single word that seems to epitomize the special features of trees is extension. Trees are markedly extended in space and time. Their extension in time is perhaps their most impressive feature to the plant breeder, for it suggests impossibly long breeding and test generations. With no

intention to be cynical, I note that the perennial habit of trees has not appreciably inhibited the annual harvest of publications by tree breeders. Longevity of trees has other consequences. It may cause the thoughtful tree-breeder to ponder the question of climatic change and its possible effects on such phenomena as fir die-back (Tannensterben) in central and southern Europe.

The tree breeder must indeed, in the words of Gifford Pinchot, "take a long look ahead". But longevity has its advantages. A tree genotype is available to a succession of breeders in the form of a single long-lived individual or ortet, and is potentially immortal in the form of the ramets of a clone. This is, of course, true of certain grasses as well. Clonal propagation, rather readily accomplished for virtually all trees, enables the breeder to extend biotypes indefinitely in space, time, and number of individuals for testing and breeding. Moreover, it is of special significance to the resistance breeder, for it enables him to perpetuate by isolation biotypes susceptible to killing diseases, and thus to have on the shelf stable biological reagents for the study of races of pathogens or the identification of injurious agents such as air pollutants (Berry and Hepting, 1964).

The perennial habit of trees, considered apart from simple longevity, makes things generally difficult for the tree breeder, for it usually means that a tree is from 2 to 20 years old and correspondingly large before it flowers. The size of reproductively mature trees makes environmental control difficult and expensive and thus limits the tree breeder's ability to control flowering time, to facilitate certain crosses and distribute the pollination work load over time. We are gradually chipping away this roadblock as our knowledge of flowering biology increases.

Trees are obviously extended in space. To look on the bright side first, this has the consequence of keeping tree-breeders fit, or in practice as riflemen, or both. Tree breeders see many views denied to others and, because people and birds are unused to finding people in trees, tree-breeders who are not excessively single-minded have unusual people- and bird-watching opportunities. The vertical and horizontal extensions of a tree have the effect of placing the same organism in several micro-climates simultaneously. This is especially significant to the pathologist. In addition, the very size of a mature tree crown aggravates the task of certifying a tree as being symptom-free. This is especially true of white pine blister rust, with the size problem compounded by time. For old infections may persist many years and remain cryptic to all but the sharpest-eyed pathologist or the most perceptive squirrel seeking succulent canker tissue to gnaw. I have discussed elsewhere more fully the space-time problems in tree breeding and some possible partial solutions (Duffield, 1963).

Trees, in general, share with man a long history of non-domestication, from the breeder's point of view. With a few exceptions like the date palm, trees have managed, until Dr. Schreiner and very few predecessors went to work, to remain above the brave new world of organisms genetically remodeled by man. This means that, in general, trees have a store of genetic variability that has been neither sorted out nor dissipated. They therefore offer the resistance breeder both challenge and opportunity.

Adequate seed production is a characteristic with high survival value for trees, as for other plants. Crop plants, however, have in most cases been rigorously selected for high seed production. Forest tree populations

exhibit wide variations in reproductive activity. As a consequence, tree breeders making selections in wild populations often find that otherwise valuable phenotypes are sub-normal seed producers. Bergman (1968), using data on flowering of 15 clones in a seed orchard of *Pinus taeda* L., reports that the two heaviest cone-producing clones will be parents of at least 50 percent of the progeny from the orchard.

Conifers are rather special trees. Historically, except for living fossils like *Gingko* and second-rate imitation trees like cycads, conifers are the oldest trees. Moreover, the best-attested records of longevity of trees belong to conifers. Conifers, with the exception of *Sequoia*, *Juniperus* and *Pseudotsuga*, have shown little tendency toward cytogenetic adventures. The diploid number of 24 chromosomes is very widespread--in fact almost universal in the family Pinaceae, except for Douglas-fir. The pines have proven rather successful in their resistance to induced polyploidy; most polyploid and aneuploid pines are phenotypically sub-normal and of reduced viability.

Conifers are predominantly cross-pollinated by wind. They produce pollen abundantly in catkins which are easy to collect. The pollen is easily extracted and may be used successfully in artificial pollinations. five years or more after collection, provided it has been properly extracted and stored. The flowering of most conifers is usually compressed into a very short period each year, except for some of the so-called multi-nodal pines that produce megasporangiate strobili over a period of several weeks. This compression of flowering, and the meiotic processes preceding it, into a short period each year keeps the conifer cytologist alert and the conifer breeder intensely busy for short periods.

Most conifers are monoecious, although some do not become so until rather late in life. Selfing does occur naturally, and some individuals produce selfed progenies which are not markedly inferior in vigor to out-crossed progenies. Possibilities for development of inbreds, with subsequent hybridization of inbreds, exist and are being explored, especially in *Pseudotsuga*.

Most conifers require one season from pollination to seed maturity, but *Cupressus* and most pines require two seasons. A few pines require three. The longevity of the male gametophyte in these cases fascinates speculative botanists, and the technical problems of keeping legible tags attached to exposed portions of tall trees in wind-swept terrain are considerable, to say nothing of wear and tear on the patience of the tree breeder. Seed of most conifers retains viability well for at least five years; for some pines, more than 30. This is an advantage conifer breeders have over those who work with some of the angiosperm trees. Seed dormancy in conifers and particularly in some of the white pines requires stratification treatments lasting as long as 90 or more days. As a result, the white pine breeder's planning flexibility is restricted. The first season's growth of most conifer seedlings is slow. This is particularly true of the white pines, which do not really enter the rapid growth phase for several years (Bingham, Hoff, and Steinhoff, in press). Corresponding to this slow tempo, the development of rust symptoms and resistance-reactions, even by seedlings infected early in life, is relatively slow. This poses problems in testing as well as in planting practice with the southern pines. The facts that rust mycelium may persist in pine tissues for several years before aeciospores are produced and that aeciospore production resulting from a single pine infection may continue for many years have important implications for the spread and control of these

diseases. When the question of rust races is attacked, the relatively long cycle of the pathogen will constitute a serious technical problem.

So far, I have been discussing some of the inherent features of trees in general and conifers in particular. Equally important are some of the characteristics of forestry which affect both disease processes and the constraints under which the breeder operates. An article of faith which underlies many of the attitudes and practices of foresters is the concept of sustained yield. While it must be admitted, as Duerr (1967) has pointed out, that adherence to this doctrine may induce excessive rigidity in the thinking of foresters, it is also evident that the concept is useful as a safeguard against expediency and irresponsibility. In any event, foresters are usually committed to the notion that the areas in their care are to be maintained as forest over an indefinitely long period. This notion imparts certain characteristics to forest management.

The concept of growing stock is fundamental to forest management. It means that the cambium of the trees composing the forest is the essential productive facility or capital. Since this cambium does not become practically effective in producing wood in significant volume or quality until the trees it envelops have reached appreciable size and age, growing stock cannot be built up quickly, nor can sudden changes in the nature of the growing stock be made. The contrasts with the nature of most agronomic crops are obvious. Forest management exhibits much greater stability--or inertia--and is therefore more seriously disrupted by killing diseases and other destructive agents than are many sorts of agriculture.

The inertia of forest management is reinforced by a tendency to rely on so-called natural regeneration in many instances. Where such reliance is total or predominant, the scope for genetic intervention is virtually nil, although skillful conservative silviculture may avoid dysgenic changes in the forest. Obviously naturally regenerated forest may prove a useful starting point for a program of resistance breeding, but application of the results depends on artificial establisment of the new crop.

Pure cultures of trees, as of any other organisms, have various ways of bringing about their replacement by something else. The practical recognition of this in agriculture is crop rotation. A common solution in forestry is the impure culture or the mixed stand. This has interesting consequences for the relationship between host species and disease. On the one hand, it tends to maintain a constant host population or substrate for the disease. On the other, it dilutes the impact of a single disease on the forest as a whole.

Forests may have high esthetic values and the public has increasingly high critical standards of forest esthetics. This is not to imply that many farm landscapes are not beautiful. However, forests are often closely associated, in fact and in the mind's eye, with mountains and with water, and this association raises the expectations and heightens the sensitivity of the onlooker. Maintenance of the esthetic values of the forest is also associated with the features of forestry I have just enumerated--continuity, diversity, and something called naturalness. The esthetic aspect of forests has its interesting implications for the resistance breeder. So-called artificial control programs, especially those involving aerial applications of chemicals, are under increasing fire from the public. The ribes eradicator, protecting white pines in our National Parks from blister rust, has had to work stealthily and with only partial approval of the park visitors. His successor, attempting to introduce resistant trees into so-called natural habitats, may anticipate similar problems.

Changes in the technology of converting wood to useful products may be large and sudden, with consequent sudden changes in the relative values of the tree species composing a forest This obvious fact has led to the argument that disease-threatened species are replaceable. The history of American agriculture records several major shifts in crop production caused, at least in part, by biotic enemies of crop plants. Nevertheless, it may be fairly argued that the situation in forestry is different, at least where an indigenous host species is involved. Most of our agricultural crop plants are to some extent exotics. Their loss from cultivation in a particular area is not an impoverishment of our biological endowment. Our indigenous forest tree species are uniquely adapted to growth in specific areas and some of them cannot be moved to escape their enemies. There is only short-term monetary justification for allowing indigenous species to become extinct or rare, one by one.

White pine forests and forestry have distinctive characteristics, mostly related to the fact that these forests are found almost exclusively in mountainous or glaciated terrain. (Any of the world's white pines could have aptly been named *P. monticola*.) Much of the area has numerous micro-climates which are especially favorable to spread of white pine blister rust, specifically the heavy fogs of early autumn when transmission from ribes to pine occurs. The mountainous or glaciated terrain also tends to accentuate the features of forest management noted above, namely reliance on natural regeneration and the maintenance of mixed stands. The white pine regions of North America are among our most scenic areas, either as settings for lakes or as easels on which the forests are held up to view. In either case, public scrutiny is intense and becoming more so. As a seral or pioneer species, *Pinus monticola* Dougl. forms important stands following the many and extensive fires which have occurred in several of the broad habitat types delinated by Daubenmire and Daubenmire (1968) in the northern Idaho--eastern Washington region. This habit is shared by *P. monticola* elsewhere in the west, and *Pinus strobus* L. has reached high levels of economic importance as a pioneer species following fire and land abandonment on many types of habitat throughout its much larger region in eastern North America.

Aside from the occurrence of white pines over a very wide spectrum of environments, we have evidence that, not surprisingly, local populations have become adapted to local environments. How local these may be is suggested by a study by Bingham and Squillace (1958) which showed evidence of localized ecotypes adapted to differences in aspect and to environmental variables found within a north Idaho area measuring less than 30 by 24 miles, but including white pine populations on sites ranging from 2700 to 5000 feet above sea level. Bingham and Squillace's evidence on aspect races of a conifer growing in mountainous terrain has recently received support from similar findings of Hermann and Lavender (1968), who studied aspect races of Douglas-fir in southwestern Oregon. These are simply two of a number of studies which are revealing important clinal and ecotypic variation in forest tree populations in mountainous regions. It is important to note that many of the respects in which these ecotypes and clines exhibit variation are revealed in growth and survival of seedlings--a matter of obvious concern in the development of disease-resistant types for planting. We have therefore not only a wealth of breeding materials, but a plethora of environments requiring adapted resistant trees.

These characteristics of white pine trees and forestry influence both the strategy and tactics of resistance breeding. Another important influence is the nature of the host-parasite relationship, specifically the

amount of genetic variation in infectivity of the pathogen and in susceptibility of the host species. At present, we have rather limited evidence bearing directly on this question, other than the successes which have been achieved in current breeding programs. Of particular interest is the question whether white pine blister rust resistance transferred from Eurasian white pines may offer protection against a wider spectrum of races of the pathogen than resistance recovered from indigenous pine populations. Until we have experimental evidence, speculative answers may be of some value in planning breeding strategy. One line of speculation follows.

In the early 20th century, *Cronartium ribicola* J.C. Fisch. ex Rabenh. did not exist in North America, but pines susceptible to this parasite existed in North America and Eurasia. The consensus of evidence and conjectures on the origins of pines postulates an Arctic origin, with southward migration in North America and Eurasia (Mirov, 1967). Mexico appears to have been a secondary center of active speciation. By the beginning of the historical era, American and Eurasian pines were disjunct. To account for the relations between white pines and *C. ribicola* in the early 20th century, there are three logical hypotheses:

(1) Extinction of *C. ribicola* in America after it came to America with pines or after it went to Eurasia with pines.

(2) Migration of pines to America, leaving *C. ribicola* in Asia.

(3) Development of *C. ribicola* in Eurasia after pines migrated to America or after they arrived in Eurasia.

A fourth, no doubt trivial, hypothesis is that the parasite existed before the host. Leaving this one aside, it is possible to work with the first three. The reactions of American white pines to *C. ribicola* suggest that host and parasite had met before. Therefore the hypothesis of evolution of *C. ribicola* after migration of white pines between Eurasia and America seems implausible. Hence it seems likely that there has been a long period, prior to the present century, when *C. ribicola* had the opportunity and was under evolutionary pressure to develop races to cope with resistance mechanisms in its Eurasian host species. The introduction of *C. ribicola* to America presumably brought a small number--perhaps only one--of these races. This race, or these few, have had little time, especially in view of the relatively long cycle of this parasite, to evolve new races. Thus it may be reasonable to expect that Eurasian white pines have a more comprehensive resistance to *C. ribicola* than the American species, and that resistance transferred to American pines by hybridization may be of longer practical duration than resistance already existing in American pine populations. This supposition is partly testable by growing resistant American lines under exposure to the pathogen in Eurasia.

With reference to *Cronartium fusiforme* Hedgc. & Hunt ex Cumm., it is interesting to note that the host species, principally *P. taeda* and *Pinus elliottii* Engelm., appear to be related to the hypothetical Mexican center of pine speciation, having no relatives in Eurasia, just as the alternate hosts, oaks of the sub-genus *Erythrobalanus*, occur only in America and are also especially numerous in Mexico.

The characteristics of the breeding materials and problems I have been discussing could be summarized in several ways. I have chosen to summarize them so as to support my strongly held prejudice that breeding

for resistance to white pine blister rust should be on a very broad genetic base. Before proceeding with this summary, I will try to explain what I mean by breadth in this instance. This is simply the inclusion of a very large number of resistant candidate trees in the base population to cover the diversity of ecotypes in the white pine regions and to select within these ecotypes a large number of phenotypes with good growth and quality characteristics. The expression "large number" in both cases is left unspecific, but it is intended to indicate a large gene pool as a hedge against development of new pathogen races and the probable invasion of new biotic enemies.

All this may be interpreted as a large unwieldy tandem selection scheme. I would only suggest that several features of trees as breeding materials make it possible to retain flexibility in adopting breeding strategies. The long life and cloning capacity of trees makes it possible to put genotypes on the shelf for indefinitely long periods. Additional flexibility is provided by the relatively great longevity of pine seed, and the abundance and longevity of pine pollen. The size and durability of trees make them easy to file and recover, provided one has the space. Even the space requirement is not a total liability. It is possible to combine forest production with breeding (Duffield, 1963) because of the space and time extensions of trees which in effect makes each one an easily recognizable individual--even more so than the members of a large animal herd, for trees don't move.

I hope I have indicated that the resistance breeder working with trees is not critically limited by the nature of his materials. His success, like that of the agricultural plant breeder, depends on the will to get the job done, expressed in financial support and the cooperation of those who use his product.

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FLOOR DISCUSSION

BINGHAM: Dr. Duffield, while you were discussing monocultures and their problems, it occurred to me that there are several blister rust resistance breeders in the audience who are faced with one sort of monoculture problem at this moment. Gerald Barnes who is working in the Forest Service, Region 6, white pine blister rust resistance program at Cottage Grove, Oregon, and Dr. Bohun Kinloch and Gaylord Parks who are cooperating in a similar Region 5 program in northern California have recently, tentatively identified single (dominant), major resistance genes in Oregon *Pinus monticola* and *Pinus lambertiana* Dougl. (Region 6) and California *P. lambertiana* (Region 5). I would like to hear some remarks by these men on how they intend to use this single dominant gene, avoiding "monoculture" problems of the type associated with such single, immunity-imparting genes.

DUFFIELD: I suspect the question will carom off the panel; at least I hope it will.

KINLOCH: The finding Mr. Bingham mentions is recent. We're pretty sure the mechanism of inheritance is simple but still don't consider our findings conclusive. As far as the utility of this gene (or other genes that express the same phenotype) is concerned in relation to different pathogenic races of *Cronartium ribicola*, I think the critical need now is to test them in different regions which may harbor different pathogenic races. This should be done repeatedly and over a period of time. The gene or genes should be tested in different combinations, within the species *P. lambertiana* and perhaps also with other species such as *P. strobus* to see if their behavior is the same as what we have observed under natural infection in California, or what Mr. Barnes and coworkers have observed under artificial inoculation in Oregon. The origin of this gene is of some interest. It just sort of showed up and I think we were all quite surprised. Perhaps as Dr. Borlaug and I were discussing yesterday it is a sort of a fossil gene, lingering in some parts of the host population. This relates to Dr. Duffield's remarks just a few minutes ago. Perhaps some of the North American white pines carried with them some major genes for resistance when they migrated from Asia. That's just one speculation. Now, whether there are races of the pathogen presently existing that are also carrying genes for virulence against these, is just a question that we have to answer by repeated tests over a range of geographic locations that may possibly harbor such races.

LOEGERING: The use of the expression major genes is not good. When we deal with major genes we find that some of these don't survive in cereal crops. A good example was Bowie wheat. On the other hand, if we go to barley, we have a major gene for resistance to *Puccinia graminis* f.sp. *tritici* that has survived as long as it has been known, which is 30 to 40 years. There is no evidence that the pathogen has picked up the virulence for this gene. Thus a major gene should not be discarded because there is potential for it to go out next week, but neither should it be accepted as something that is going to live with us forever. There's another side to this. Many of you know that I have been involved in the International Rust Nursery program, and I have a little experience that may be of value here. Say Dr. Pope introduced a variety of wheat that is resistant; it is resistant here in Idaho and we can't deny this. And yet that same variety taken across the mountains may be susceptible--the gene for virulence might be there. On the other hand this variety may be resistant throughout North America, or you may find that no place in

the world do you have the virulence to attack this variety. The important thing is to find out if any place in the world there is a combination that is virulent. If it occurs some place then you can be quite sure, once the resistance gene is widely used, the virulent race will come here. The further you are away from the virulence, the better off you are. Even though you can find virulence some place it's very dangerous to rely on a major gene too extensively. Now, concerning pine trees, you have a great advantage because with pine you are dealing with the haploid stage of the white pine blister rust fungus. If you have a sporidia floating around, and there is one having the proper virulence gene, you can't cover it up by a dominant gene for avirulence. In pine the rust mycelium is haploid, and you will find a recessive virulence gene immediately. Thus testing a resistant pine against populations of *Cronartium ribicola* all over the world will accomplish even more than the testing we do in cereals. Virulences in cereal rusts can be covered up in the dicaryotic stage of the fungus.

BINGHAM: To return a moment to the "major-gene monoculture" problem, Mr. Barnes, Dr. Kinloch, and their administrators have another solution. They recognize that this major resistance gene is a step forward, and also its danger. They are proposing to use it on a limited scale in plantations where the resistant white pines would be mixed with trees of other species.

CALLAHAM: This brings me to a topic that may not have been brought out enough in Dr. Duffield's presentation. What is a monoculture in Forestry? Typically, a monoculture in wheat is the planting of almost pure fields of one strain from the center of the Canadian plains to the highlands of Mexico. That kind of a monoculture, I think, never would exist in forestry for many reasons that Dr. Duffield gave. Forestry through its harvesting and regeneration processes moves from one small piece of land to another. Forestry rarely creates at one time the conditions for epiphytotics that would exist in a wheat monoculture. Here is another point. Presumably we are going to build dynamism into our tree breeding process. We will constantly be generating new varieties having different combinations of resistance factors. We can create different mixtures of resistant entities within the type that is planted. On any one mountainside, as a rotation occurs, foresters will create a spectrum of new and different resistant types. Other species may be intermingled as Duffield brought up. We really need to focus our thinking on what is a monoculture in forestry in contrast to what is a monoculture in agriculture.

DUFFIELD: I believe Dr. Callaham is correct in his suggestion that the term monoculture has different meanings in agriculture and in forestry. Foresters have generally been concerned with the effects of monoculture on soil properties and less concerned with pathological effects. We may, in the future, develop a more agronomically-oriented attitude.

BORLAUG: I would like to make two comments. One, I think this major gene that was discussed a minute ago is something that is useful and something that should be used. I think that it should be used in the context of using it in combination with the other kinds of genes you have already identified. The problem then is that when you superimpose one of these major genes--almost always a dominant--it will mask the effect of others. Therefore the problem becomes one of identifying or knowing when you still have the polygenic type of resistance underneath. My second comment concerns the remarks Dr. Callaham just made. I think you

have, and will continue to have a lot of diversity in your forest. If you handle this right hopefully you will maintain and broaden this type of diversity. You can do this through your selective cuttings to improve the type of product that you get. I'd like to interject another point--that you shouldn't breed only for rust resistance. This is a mistake that is made time and again. I have seen many plant breeders in my close fraternity in wheat that have spent a life time developing disease resistant varieties that have no value whatsoever because they don't yield.

SLINKARD: Dr. Duffield, referring to your proposal for a wide gene base within ecotypes, the phrase "within ecotypes" bothers me. I would like to get your comments, or someone else's, on the use of wide adaptation. In other words, instead of trying to get rust resistant selections for each ecotype, why not try to combine ecotypes and get a wide range of genetic variation so that one population may be adapted to a 2- or 3-thousand feet altitude range or some other ecotypic variation?

DUFFIELD: Well, I think that there are precedents that would encourage us to hope that this might be possible. We have evidence on both sides of this question. We have the evidence which I have referred to very briefly on localized ecotypes and then we have certain species which are notorious as being widely adapted, for example the Rocky Mountain form of *Abies concolor* (Gord. & Glend.) Lindl., which you find cultivated everywhere. Then there is the tree that grew in Brooklyn, *Ailanthus altissima* (Mill.) Swingle. I would hope that we could develop similar forms. Further, Jens Clausen and the Carnegie Institution group at Stanford, working with altitudinal ecotypes of *Potentilla*, were able to develop F_2 lines of extremely wide adaptability and good growth. Developing wide adaptability appears to be very much in the cards.

BORLAUG: One more comment about this adaptation, because I think it is fundamental to your long-time improvement. Again it calls for a practical point of view. You can get specificity and you can maintain it, but how are you going to use it? How are your seed programs going to be handled so that you exploit this specific adaptation? This has come up in recent years in cereal crop improvement. In Mexico we are aware of and trying to get ecotypes for a lot of small niches in the mountainous country. We gave it up and started over. Without going into detail, the new work involved growing part or all of the segregating populations at sea level and at 8500 feet, at 28 degrees latitude. The next generation was grown at 18 degrees latitude; and all those populations that didn't do well under both sets of conditions, including severe disease epidemics, were discarded. Sum and substance of all this has been that after 15 or 20 years these varieties have provoked the so-called "green revolution". Genotypes are those coming from that program in Mexico. It also became apparent that one single gene and some modifiers has been responsible for making it impossible to adapt any of the spring wheat varieties bred in Canada or the northern U.S.A. to places below 38° latitude. The Mexican varieties, however, will compete and in many cases outyield Winnipeg varieties under Winnipeg conditions. I say, be careful about specific adaptation. I recognize, however, since I did have a forestry background many years ago, that this whole question of winter tolerance, freezing and wintering is something that's not necessarily a problem in an escape variety such as spring wheat.

SPECIFICITY IN PLANT DISEASE[1]

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ABSTRACT

The development of the gene-for-gene hypothesis has served a useful function in that it has focused attention on the host-pathogen relationship (aegricorpus). As a result it is now understood that specificity is the result of the "gene-for-gene" relationship in host-pathogen associations. Specificity has been demonstrated only in cases where both host and pathogen can be propagated as clones or pure breeding populations. In general the pycnial and aecial stages of rust fungi cannot be used in studies of specificity since they are non-repeating and cannot be maintained as clones or pure breeding populations. Thus sporidia, which initiate the pycnial stage, must have the genes for high pathogenicity corresponding to any genes in the host plant for low reaction in order to produce an infection which survives.

INTRODUCTION

There is a great difference between the classical view of plant disease and the view resulting from the development by H. H. Flor of the gene-for-gene concept. Both points of view are valid and useful, and one should not be used to the exclusion of the other when approaching problems in plant pathology. Some problem areas in plant pathology remain unresolved because they have been approached only from the classical standpoint. The most prominent example is the failure to resolve the "nature of plant disease resistance". If we approached this problem by studying the "nature of the host-parasite interaction", more progress might be possible. This paper discusses the genetic nature of the host-parasite interaction which is commonly referred to as the "gene-for-gene hypothesis" and suggests how it might be utilized in studies of white pine blister rust.

The gene-for-gene hypothesis was developed by H. H. Flor from studies which he started in the 1930's. He summarized the philosphy in the title of a paper he wrote in 1955 (Flor, 1955): "Host-parasite interaction in flax rust - its genetics and other implications." In this title, the words "host" and "parasite" refer to two taxonomic groups of organisms,

[1] *Contribution from the Missouri Agricultural Experiment Station, Journal Series Number 5723, approved June 16, 1969.*

not to a plant or variety and a culture or race. The two words are used as a hyphenated adjective of the word "interaction". The interaction is the subject of the paper, not the host or the parasite. This idea is the core of the gene-for-gene concept. Specifically Flor says in his title that the interaction he will discuss is "flax rust" not *Melampsora lini* (Pers.) Lev. or *Linum* spp. The rest of the title says that the "genetics and other implications" of the interaction will be discussed and not the genetics and other implications of the host or parasite. While the genetics of host and parasite are discussed in the paper, they are not considered as independent systems.

No attempt will be made to review the data from which the gene-for-gene hypothesis was derived. The reader is directed to selected reviews which summarize some of the evidence (Flor, 1956, 1959b; Moseman, 1966; Person, 1959; Williams, Gough and Rondon, 1966). There are between 50 and 100 illustrations of the validity of the gene-for-gene hypothesis - the exact number depends on what degree of proof is desired. It seems reasonable to assume that exceptions to the hypothesis will be found, but no one, insofar as I am aware, has demonstrated a single instance where the hypothesis does not hold. Questions have been raised regarding the validity of the expression "gene-for-gene" but not of the concept itself.

There is much concern with generalized resistance of the type van der Plank (1963) called "horizontal", or more recently, "uniform" (van der Plank, 1969). Within the structure of Flor's concept of host-parasite relationships the word "non-specificity" should be applied to this idea of van der Plank's to contrast it with the specificity of the gene-for-gene relationship. In our present stage of knowledge, "non-specificity" can only be defined as a host-pathogen relationship for which specificity has not been demonstrated. While this is a circular definition it is needed to indicate our current degree of ignorance. Non-specificity is very likely a valid concept and should be studied more intensively. It is not the purpose of this paper to discuss non-specificity; however it is important that in discussing the gene-for-gene concept we do not lose sight of the fact that a host-pathogen relationship perhaps involves more than specificity.

Current definitions of "disease" in plant pathology as well as in animal and human pathology consider disease a character of the host. Disease is variously defined as a malfunctioning process of the host, a deviation from normal in the host, and economic damage to the host. These concepts are valid and useful; after all we *are* interested in a healthy plant, animal, or self. However, these definitions cannot apply to the host-pathogen relationship which is a natural and, therefore, a normal relationship. It must not be forgotten that sometimes the relationship is more detrimental to the pathogen than the host.

The idea of disease is usually expressed in diagrams in such a way that the pathogen infects the host, both are influenced by the environment, and the net result is disease which is expressed by symptoms. These symptoms express the resistance and susceptibility of the host according to whether the infection type is low or high.

THE GENE-FOR-GENE CONCEPT

In the gene-for-gene concept we deal with the relationship between host and pathogen. The relationship, the host, and the pathogen may be independently affected by environment. The result of this complex is infection type. If we retain the current definition of disease, then the infection type cannot be considered the disease, since disease is defined in terms of host symptoms, whereas the infection type also includes signs of the pathogen and additional manifestations which are characteristic of the relationship itself. The manifestation of the complex of interactions of a specific host:pathogen:environment system I have called the aegricorpus (Loegering, 1966) to distinguish it from the many views of "disease". The infection type is the character of the aegricorpus. This approach to the gene-for-gene concept, if accepted, strips our minds of the emotional involvement resulting from the expression "a diseased plant".

CATEGORY III INTERACTION

Loegering and Powers (1962) published a diagramatic model of a simple gene-for-gene relationship. Later Loegering (1966) modified this model to bring in the word aegricorpus. Figure 1 is a further modification of this model. The model introduces the terminology which I use in discussing the gene-for-gene concept. The concepts which these terms represent have been published (Loegering, 1966; Loegering and Powers, 1962). Infection type is the character of the aegricorpus, whereas reaction and pathogenicity, respectively, designate the characters of host and pathogen. The phenotypic expression of infection type, reaction, and pathogenicity is low or high. *This pair of terms is comparative.* Thus infection type 1 is low compared to infection type 2 but high compared to infection type 0. The use of low and high for reaction and pathogenicity replaces the terms resistance and susceptibility, and avirulence and virulence used in earlier published diagrams. This avoids the variable concepts which these latter terms convey to different people and also aids in the development of a new system of genetic symbolization as will be discussed later. The older terms should be reserved for describing varieties and cultures.

Seldom is it possible to determine the inheritance of reaction or pathogenicity without observing infection type. Infection type is the character of the aegricorpus, not of host or pathogen, but its expression results from interaction of the genes of the two organisms which make up the aegricorpus. Because of this interrelationship it is possible to use infection type to determine host or pathogen genotype by holding one constant.

The genotypes shown in Figure 1 for host and pathogen are combined in all combinations and are used to show the potential genotypes of the aegricorpus. The illustration uses only one gene pair for reaction in the host and one gene pair for pathogenicity in the pathogen. These pairs are called "corresponding gene pairs" and neither interacts with any other gene pair for pathogenicity or reaction. In examining the genotypes of the aegricorpus we see that low infection type results only when host and pathogen genotypes of corresponding gene pairs are for low reaction and low pathogenicity. When the genotype is for low reaction and high pathogenicity or high reaction and low pathogenicity the infection type is high. This seems incredible to many biologists but it has been demonstrated to be true over and over, and no exceptions have been found to date in studies involving obligate pathogens.

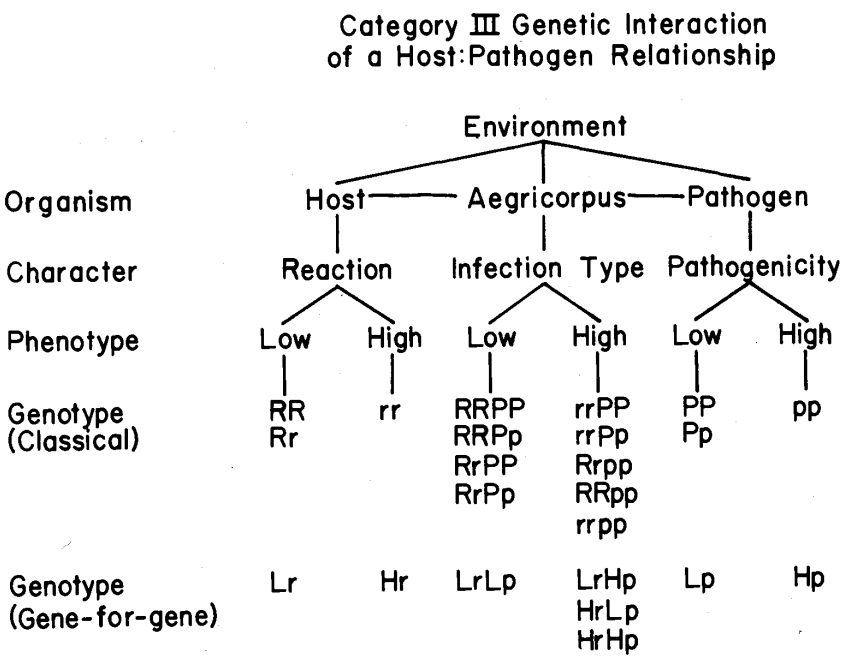


Figure 1. Diagrammatic representation of the gene-for-gene interaction between a single set of corresponding gene pairs in a host-pathogen relationship. Low reaction and pathogenicity are shown as dominant for the sake of simplicity in the diagram.

This interaction between corresponding gene pairs is referred to as a Category III interaction (Loegering and Powers, 1962). (Categories I and II are from classical genetics and represent, respectively, interaction between alleles in one organism and interaction between genes at different loci in one organism.) Sometimes low reaction and/or low pathogenicity are recessive rather than dominant as shown in Figure 1. This does not change the basic principle but if both are recessive only one aegricorpus genotype (*rrpp*) will give low infection type.

We can see then that a host gene pair for low reaction (whether homozygous or heterozygous dominant or homozygous recessive) has the potential to produce low infection type which can be designated *Lr* (where *L* is for low and *r* is for reaction), whereas a gene pair for high reaction has the potential for high infection type and can be designated *Hr*. The same is true for the pathogen with respect to the corresponding gene pair, and we can have a genotype for low pathogenicity designated *Lp* or high pathogenicity designated *Hp*. Each of the symbols refers to any combination of alleles at one locus in one of the organisms which has the potential to condition high or low infection type respectively.

Using these symbols, we find there are only four potential genotypes for the aegricorpus in a Category III interaction: *Lp/Lr* = *Lit* (low infection type), and *Lp/Hr*, *Hp/Lr*, and *Hp/Hr* = *Hit*. These can be compared to

gametic pairing of alleles (Category I interactions); e.g. aa, aA, Aa, and AA. By carrying this comparison further, we can say that in the Category III interaction *L* is recessive and *H* is dominant. This in no way implies what is recessive or dominant in the Category I interaction in host or pathogen. This peculiarity is one of the reasons for much of the misunderstanding of the gene-for-gene concept. The phenotype for each Category III genotype in a given environment is typical though not necessarily unique. Thus in considering wheat stem rust we can write *Lp*1/*Lr*1 = *Lit*1 = 1+; *Lp*1/*Hr*1 = *Hit*1 = 3+, etc. This integrity of the phenotype is extremely useful for many studies, provided there is variability in the phenotype of *Lit* for different corresponding gene pairs.

In Figure 1, the Category III genetic interaction is illustrated by use of organisms of n + n genetic constitution such as in flax rust. If in this model we dealt with a disease such as mildew of barley we would have a host of n + n constitution and a pathogen of n constitution. A model of this interaction would have only 6 of the classical genotypes of the aegricorpus instead of 9, but this would in no way change the gene-for-gene genotypes. Thus the nuclear condition of host and pathogen need not be considered in learning to understand the gene-for-gene concept. Of course the nuclear condition must be known when applying the concept in experiments.

CATEGORY IV INTERACTION

Most host:pathogen relationships involve many corresponding gene pairs. We know this because many crop plants are known to carry several to many genes for reaction. For each of these there must be a corresponding gene in the pathogen, according to the gene-for-gene concept. This is called the Category IV interaction. This is easy to visualize by use of the *L* and *H* symbolization. For example, a host plant has a genotype *Lr*1*Lr*2*Hr*3*Hr*4 and the pathogen has the genotype *Lp*1*Hp*2*Lp*3*Hp*4 (the numerals refer to loci). If we put the pathogen on the host we have:

$$\frac{Lp1\ Hp2\ Lp3\ Hp4}{Lr1\ Lr2\ Hr3\ Hr4}$$

From our discussion of the Category III interactions we know that *Lp*1/*Lr*1 = *Lit*1, *Hp*2/*Lr*2 = *Hit*2 *Lp*3/*Hr*3 = *Hit*3, and *Hp*4/*Hr*4 = *Hit*4. What is the result of the system shown? All evidence to date shows that *Lit*1 will be expressed or, we might say, be epistatic to the other Category III interactions which would give a high infection type. This is why a single gene for "resistance" is effective so long as the pathogen does not have the corresponding genotype for *Hp*.

A host:pathogen relationship often has two corresponding gene pairs for *Lit*. Such a situation can be illustrated as follows:

$$\frac{Lp1\ Lp2\ Lp3\ Hp4}{Lr1\ Lr2\ Hr3\ Hr4}$$

Corresponding gene pairs 1 and 2 are both for *Lit* and therefore epistatic to *Hit*3 and *Hit*4. Expression of *Lit*1 *Lit*2 might be in two ways. We will assume that *Lit*1 = infection type 1+ and *Lit*2 = infection type 2-. Infection type 1+ is lower than 2- and would usually be expressed--and thus be epistatic. Cases are known where the combination of two *Lit*'s in one system will result in an infection type lower than either of the Category III interactions involved. In the assumed system shown above the infection type of the aegricorpus might be 0. In this case the two Category III

interactions (*Lit*1 and *Lit*2) interact in a complementary manner to produce an infection type neither produces alone and can be compared to Category II interactions. Thus there is a parallel between Category I and II genetic interactions of classical genetics and Category III and IV genetic interactions peculiar to host:pathogen interactions.

This gives the essentials of the gene-for-gene concept. Much more could be written concerning problems of incomplete dominance of genes in host and/or pathogen, reversal of dominance in reaction, cytoplasmic inheritance, *Lit*'s which singly are expressed as "high infection type", reversal of models when we work with systems which include facultative pathogens, the questionable existence of alleles for high reaction, the vast confusion in the area of physiology of host:pathogen systems, temperature effects on expression of the aegricorpus, the relationship of the gene-for-gene hypothesis to the physiologic race concept, progressive increase in virulence, and many other areas. It perhaps need only be said that the gene-for-gene concept is a potentially powerful tool in shedding light on some of these question -- and that is its importance.

SPECIFICITY IN WHITE PINE BLISTER RUST

There is no reason to believe that the gene-for-gene relationship does not hold for white pine blister rust; however, its application to practical problems of protecting pine from this disease has peculiarities. This is because (1) the non-repeating pycnial-aecial stage of the fungus is the one which causes the economic damage which we wish to control, and (2) we do not know whether some of the genes for pathogenicity in the uredial host:pathogen relationship are the same as in the pycnial-aecial host:pathogen relationship or whether these two relationships depend on different genetic systems in the pathogen.

In nature the pycnial and subsequent aecial stages of *Cronartium ribicola* J. C. Fisch. ex Rabenh. do not normally spread from plant to plant of the same species (are non-repeating) although under controlled conditions this might be achieved. Thus, when a sporidium of *C. ribicola* falls on a pine needle, germinates, and initiates infection, it must have the right genes for high pathogenicity or it will be unable to carry on through the life cycle. For this reason we can say there is absolute selectivity for those sporidia which have all the genes for high pathogenicity corresponding to all the genes for low reaction which a particular pine tree carries. Thus, in the ecological association of *Pinus*, *Ribes*, and *Cronartium*, infection by a given sporidium developed from a teliospore produced on *Ribes* might induce high infection type on one pine tree but low infection type on another and vice versa. It is obvious that this can't be tested directly, but it might be possible to obtain evidence by grafting or "inoculation" with tissue cultures.

Assuming that a gene-for-gene system does exist in the pycnial host: pathogen relationship, only those genotypes of the pathogen will survive which have the necessary genes for high pathogenicity corresponding to the genes for low reaction in the host plant. This selectivity of certain pathogen genotypes has been observed in the uredial host:pathogen relationship for the wheat:*Puccinia graminis* Pers. f.sp. *tritici* Eriks. & E. Henn. and flax:*M. lini* relationships. Sears, Loegering, and Rodenhiser (1957) discovered a gene in wheat for low reaction which was found to be almost universally present in wheat varieties grown in the United States. As a result, cultures of the pathogen are seldom found in the field which do

not have the corresponding genotype for high pathogenicity (Loegering and Powers, 1962). Flor used Bison flax as his "universal suscept" (Person, 1959). In Australia Kerr (1960) found cultures of *M. lini* which are avirulent on this variety, indicating that Bison does have at least one gene for low reaction and the population of *M. lini* in the United States is homogeneous for the corresponding gene for high pathogenicity.

All accumulated evidence related to the gene-for-gene hypothesis has been obtained from host:pathogen relationships in which the vegetative or repeating stage of the fungus has been studied, whereas the sexual part of the life cycle of these pathogens is not significantly involved in producing damage to the economic host. In the case of blister rust, however, it is the pycnial and aecial stages (non-repeating stages) of *C. ribicola* with which we are concerned. The work of Flor involved a fungus which is autoecious--having all stages of the life cycle on one host species--but the vegetative (uredial) stage, which is the damaging stage, was studied. One study (Flor, 1959a) of the pycnial and aecial stages is of considerable interest. Flor induced sporidial infection from teliospores of a culture of race 201 of *M. lini* on the Bison and Bombay varieties of flax. Using the resulting pycnia, he made 5 selfs on Bison and 38 on Bombay from which he obtained aecia. All 43 cultures were virulent on Bison but all were avirulent on Bombay. Thus Bombay behaved like an aecial host. These results could be obtained as a result of a single gene difference between Bombay and Bison.

Puccinia graminis tritici is a heteroecious fungus, and it is the uredial stage which occurs on the economic host (wheat). It is this stage in which the extensive specialization is found as a result of numerous corresponding gene pairs for reaction and pathogenicity. In general its pycnial host, barberry (*Berberis* spp.), is "susceptible" just as white pine is "susceptible" to *C. ribicola*. Some cultures of *P. graminis tritici* have been shown to be avirulent to barberry (Green and Johnson, 1958; Johnson and Green, 1954), which indicates that there might be a gene-for-gene relationship between barberry and *P. graminis tritici* just as there is between wheat and *P. graminis tritici*.

The relationship between host and pathogen sometimes becomes confused by the taxonomic classification of the host and/or the pathogen. The two blister rust fungi, *C. ribicola* and *C. occidentale* Hedgc.,Bethel & Hunt, might be considered the same species since both alternate to *Ribes*. spp. There are some morphological differences between them, but they are differentiated mainly by the fact that their pycnial-aecial hosts are different pine species. The two Peridermium rust fungi, *C. fusiforme* Hedgc. & Hunt ex Cumm. and *C. quercuum* (Berk) Miyabe ex Shirai, can be differentiated by the reaction of *Quercus velutina* Lam. to the uredial stage of these two fungi (Dwinell, 1969). Low infection type results from *C. fusiforme:Q. velutina* and high infection type results from *C. quercuum: Q. velutina*. However, *C. quercuum* can be divided into two physiologic races by the differential reaction of *Pinus banksiana* Lamb. and *P. virginiana* Mill. to infection by sporidia (Powers, in press).

In leaf rust of wheat d'Oliveira (1966) has shown that in Portugal *Puccinia recondita* Rob. ex Desm. f.sp. *tritici* can be divided into two groups by the differential reaction of the aecial hosts, *Thalictrum speciosissimum* Loefl. and *Anchusa italica* Retz. Cross fertilization of pycnia on these two hosts has not been possible. This specialization on the aecial hosts does not appear to be related to the specialization of the uredial stage of the fungus on wheat. If we compare leaf rust of

wheat and the two *Ribes*-alternating blister rusts of pine, we find two aecial hosts and one uredial host involved in both cases. However, taxonomists have separated two species of pathogens involved in the two blister rusts but only one species in leaf rust of wheat. Yet in both cases the variability in the host:pathogen relationship could be explained on the basis of two corresponding gene pairs. There is no evidence that this is true, primarily because of our inability to transmit the pycnial-aecial stage from plant to plant.

Obtaining direct evidence by the use of grafts or tissue-culture inoculations may be possible. If so, the methodology suggested by Loegering (1968) could be used to predict the presence of gene-for-gene relationships in pycnial-aecial host:pathogen relationships. Moseman (1966) has reviewed another approach to this problem. Work with barley mildew (*Hordeum vulgare* L.:*Erysiphe graminis* D.C. f.sp. *hordei* Em. Marchal) has demonstrated clearly that the genetics of one member of the relationship can be determined by study of the genetics of the other member.

Nelson and Kline (1963) worked with leaf spot of corn (*Zea mays* L.: *Helminthosporium carbonum* Ullstrup) and leaf blight of oats (*Avenae sativa* L.:*Helminthosporium victoriae* Meehan & Murphy). Reaction to these pathogens is controlled by one gene pair in each of the hosts; however, they cannot be crossed to study the relationship of the 2 pairs of genes. *H. carbonum* is avirulent on oats and *H. victoriae* is avirulent on corn. Nelson and Kline were able to cross the 2 pathogens and obtained a segregation of 1:1:1:1 for haploid ascospore cultures with high pathogenicity to both hosts, high pathogenicity to corn but low to oats, low pathogenicity to corn but high to oats, and low pathogenicity to both hosts. From these data we can conclude that the 2 gene pairs in the respective hosts are different. D'Oliveira (1966) attempted to do this type of experiment involving the aecial host:*P. recondita* Rob. ex Desm. f.sp. *tritici* (Eriks.) Carl. relationship, but he was unable to cross either the hosts or the pathogen cultures involved. A similar situation exists with respect to the two *Ribes*-alternating blister rusts of pine. All attempts to cross pinyon pines with 5-needle pines have failed (C. W. Busche, *personal communication)*, and I am unaware of any attempts to cross the two pathogens. Thus the possibility of a gene-for-gene relationship involving these two pine rusts has not been tested.

Clearly defined evidence for or against the occurrence of a gene-for-gene relationship between white pine and *C. ribicola* is not available. Yet the illustrations indicate procedures and points of view which could be useful in obtaining evidence. Such evidence, whether for or against would be useful in attempts to control damage to pine by blister rust.

Attempt has been made to acquaint the reader with the gene-for-gene concept and point out what a powerful tool it is in studies of any host: pathogen relationship. To utilize it to its maximum in studies of blister rust, foresters and forest pathologists must consider the aegricorpus as well as the fungus and the diseased tree. This approach could be extremely useful even if the relationship of pine:*C. ribicola* is found to be non-specific.

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FLOOR DISCUSSION

BINGHAM: Dr. Loegering, why can we not identify a race in blister rust by simply passing it back through the ribes and continue a genetic analysis thereafter?

LOEGERING: The answer to your question involves a definition for the word race. Races are identified on specificities and colonal propagation of host and pathogen or non-segregating populations are necessary. Now, if you can produce a non-segregating line--for instance if your pathogen is homothallic as has been suggested here, and by some of your work, then this homothallism can be used in this respect. Also, you could demonstrate specific races by grafting or with tissue cultures by using them for inoculum since they are clones. You must be able to inoculate two different plants with the same sporidium somehow or another. If your pathogen is homozygous then you have no segregation and this can be used as you suggest. There are several men who are working on the smuts here today. Their concept of a race in smuts is so different from that for the cereal rusts that it is hard for us to communicate. The point that I would make, however, in all of this is that in blister rust forget about races and use the genes instead of the race concept. I would jump the race bridge. I wouldn't monkey with it.

GERHOLD: Dr. Loegering, in your model does low infection include no infection?

LOEGERING: No, because an aegricorpus is what you use to determine these things and if you have no infection you have no aegricorpus.

GERHOLD: Can the condition of no infection be incorporated in the concept then?

LOEGERING: No, because you have no disease if you don't have a pathogen. If we have a pine tree growing out here and there are no ribes and no sporidia around then you should not include this in the disease concept. Escape, which you are dealing with here, is another thing. It has nothing to do with the gene-for-gene relationship.

GERHOLD: I didn't want to include escape here but I did want to refer to a possibility of a gene whicn would confer immunity. How do we deal with this?

LOEGERING: I, first of all, would ask you to define what you mean by immunity because I do not believe that such a thing exists.

PERSON: May I interrupt here?

LOEGERING: Go ahead.

PERSON: I think the question concerned a gene that conferred resistance because it prevented the fungus from infecting the host.

LOEGERING: Then you are dealing with something like klenducity, for example escape, because the pine trees have wax on the needles or something of this type. This might be the result of a single gene but this would be universal and I am quite sure I would include it under non-specificity. Dr. Zadoks, would you want to comment on the separation here of ideas on general resistance?

ZADOKS: In general, I conform with your ideas.

PERSON: I think you would be in trouble, Bill, if you had to accommodate this kind of gene whose action was to prevent infection so that the fortunate tree with this gene just never was infected. For one day a race of the rust could come along that could handle this gene and infect. How would you then fit this into your idea of the aegricorpus?

LOEGERING: Well, we might do a little juggling at that time, if you find the situation occurring.

KINLOCH: I wonder how useful the gene-for-gene concept is in the case of an exotic disease on a native species.

LOEGERING: The gene-for-gene concept is only valuable for purposes of thinking and I tried to emphasize this. The gene-for-gene concept does not change the methods that you use in doing your plant breeding. The methods you use to handle your pathogens, and so on. But, it is useful in the analysis of information and that sort of thing. It makes your observations so much more meaningful. I want to emphasize very strongly that what we are dealing with here is a revision of the way we look at disease. That's what it amounts to and it is this revision of point of view that the gene-for-gene concept has given us. But, the gene-for-gene concept as a method of plant breeding hasn't added much. It has made it easier to understand what's happening and that is why I limited the gene-for-gene concept. To me it's very helpful. Now, you get into the exotic diseases. Well, maybe there are no gene-for-gene relationships because of the things you mentioned. That doesn't make any difference in the whole system, but if there are any you see them. I'd like to comment on something that Dr. Duffield had said. I was going to mention this in my paper but I didn't get over half of what I was going to say. The question of where the blister rust came from and where *Pinus monticola* Dougl. came from is important. At the present time we have a world survey underway in order to determine something of a basic nature. Is it or could it be true that the center of origin of your host is in region A, the center of origin of your pathogen is in region B and the center of origin of the disease is where regions A and B overlap? I would suggest that you might apply this point of view to thinking about centers of origin. This is only one way of thinking, but to think about things this way comes from an understanding of the gene-for-gene concept itself. The origin of the disease might not be in either the center of origin of the pathogen or the host.

MCDONALD: We have a rather unusual situation with white pine blister rust in that resistance mechanisms can be separated in time and space. This relates to your infinite selection idea. We have the possibility of a resistance factor in a secondary needle, in the stem, or in the primary needle or traumatic simple leaf as it is sometimes called. Since there are three separate infection courts, resistance mechanisms can be bypassed. This means that the idea of infinite selection must be expanded to include several levels. That is a type or race of *Cronartium* that may be avirulent on the secondary needle could establish an infection and produce aeciospores on that plant by entering through primary needles. It's just one more thing we have to consider.

LOEGERING: This was the subject of a rather lengthy discussion last night regarding smuts because you determine what you want to know by the percent of smutting. You don't know what happens in infected plants until

you see the symptoms in the head. This is similar to what you are referring to. I would like to also comment on your first statement. You said you have an unusual situation in blister rust. I say you have an unusual situation in every combination of culture and variety that you deal with in this area. I only gave a simple illustration of a single combination and I mentioned all the other areas that vary one way or the other. They all fit into the concept and I have never found any of them that don't.

GERHOLD: You indicated that environment does modify infection type. How much difficulty would this cause in trying to distinguish between the different infection types? Do they overlap?

LOEGERING: There are a whole series of answers to your question. I will start out with one and I may end up by giving a different one. For instance, we have a gene called Sr 6 and a corresponding gene Psr 6. This combination will vary from zero flecks up to what we call a type four over a temperature range of about seven degrees. It's one of the beautiful illustrations of what you are talking about. It is repeatable and there is no problem. This very thing can be used in genetic studies because regardless of what the genetic constituion of the host and pathogen are, with respect to this combination, by growing it at a high temperature you eliminate the combination from your system and it thus can be used positively in studying other genes. Now, your question about differentiating infection types. I mentioned when I was talking, that the infection types are characteristic for each combination but may not be unique. Different corresponding gene pairs may give you the same infection type as far as the eye can tell, but it is characteristic of each particular corresponding gene pair. If you are dealing with two corresponding gene pairs giving the same infection type you would get a normal segregation of 16 to 1 in either the host or the pathogen. Whereas, if you had two discreet infection types which are characteristic and unique in that particular system, you would get a 12-3-1 segregation.

PERSON: I would like to add that there are certain genes for resistance to the stem rust in wheat that I know are temperature sensitive. Now, there is a great deal of talk about Ts mutants in bacteria and, more recently, *Drosophila*, but temperature sensitivity for resistance genes has been known for quite some time. Studies have shown that a difference of as few as five degrees, Fahrenheit, will make the difference between resistance and susceptibility. That is with a rise in temperature of five degrees Fahrenheit the plant that would have been resistant now becomes susceptible, so that there are some problems associated with temperature.

LOEGERING: On the other side there are certain combinations which don't change, regardless of what you do with temperature and environment.

PERSON: If you had a temperature-sensitivie gene in a wheat plant together with another one that wasn't temperature sensitive, and then you raised the temperature beyond the threshold for sensitivity, would the other gene, the stable one, still express itself?

LOEGERING: Yes and there is a paper on this. I used two sensitive gene pairs and one non-sensitive, and you could determine the genetics by using only changes in temperature and cultures and not making any crosses. I might mention that one thing to come out of this was the quadractic check. Working with wheat mildew, Slesanski and Ellingbo of

Michigan State found through use of the quadratic check that high infection type resulting from low reaction and high pathogenicity is not the same physiologically as high infection type resulting from high reaction and low pathogenicity.

REFLECTIONS ON DISEASE RESISTANCE IN ANNUAL CROPS

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ABSTRACT

Assessment of partial resistance uses typological and quantitative methods. Epidemiological theory suggests several parameters that can be counted or measured, the so-called "components of resistance". Laboratory tests with single plants are "monocyclic" tests; race nurseries are "continuous monocyclic" tests. For "polycyclic" tests, involving populations of plants, specially designed field experiments are needed. The "one cultivar - many races" test leads to a "resistance spectrum" in which uniform resistance, differential resistance or both together can be discerned. Differential resistance is mono- or oligogenic; uniform resistance polygenic. Environment can influence gene expression. Natural selection for resistance uses polygenes and leads to uniform resistance, an example to be followed by breeders. Breeding for differential resistance is easy but differential resistance tends to be self-destructive. To control white pine blister rust, monogenes are not advisable but risks may be reduced by the "composite design" and the "mosaic design". Breeding for polygenic partial resistance is nature's own method; it is the safest way to improvement; significant interactions between environment and resistance (gene expression) should be utilized when available. Many factors can interact to reduce the relaxation time of an ecosystem unbalanced by the introduction of a pathogen.

INTRODUCTION

Disease resistance is a desirable character which the breeder wants to incorporate into his new synthetic plant types. All too often, disease resistance is regarded as a qualitative character. The resistance is either present and no disease symptom becomes visible, or it is absent and plants become fully diseased after infection.

This picture in black and white is misleading. A newly emerging philosophy looks at disease resistance as a quantitative character, that is a character which can assume all grey tones from pure white to raven black. It is the art of the pathologist to measure the grey tone value correctly. The possibility of accurately assessing intermediate forms of resistance opens the way to new techniques of resistance breeding.

MEASUREMENT OF RESISTANCE

PARTIAL RESISTANCE

The pathologist studies his pathogen by making isolates. Ideally, each isolate is the genetically uniform clonal offspring of one single cell. Different isolates may or may not have identical genomes.

A test plant is tested for resistance by inoculating it with an isolate under standardized conditions. In this "one isolate - one plant test" one of the three following reactions can be expected:

a. The plant remains healthy, resistance is complete.
   Numerical value of resistance RES = 1.

b. The plant becomes as diseased as the most susceptible control.
   Numerical value of resistance RES = 0.

c. The plant shows an intermediate reaction.
   Numerical value of resistance 0<RES<1.

In the latter case the resistance is said to be "partial".

TYPOLOGICAL AND QUANTITATIVE ASSESSMENT

There are two methods of disease assessment: The typological and the quantitative method. The typological method uses a descriptive key to characterize two or more classes of reactions denoted by symbols or figures (see Fuchs, this proceedings). The observed disease reaction is placed in one of these classes. Classification is easy in flax rust (*Melampsora lini*)[1], where the choice is between diseased and healthy, but difficult in cereal rusts, where five main classes arbitrarily subdivide a continuous range from absence of symptoms to severe disease.

The quantitative method chooses characteristics which can be measured or counted, e.g.:

a. Infection ratio--the number of resulting lesions divided by the number of spores applied.

b. Latent period--the period from inoculation until first production of spores in the resulting lesions.

c. Sporulation rate--the number of spores produced per lesion, per unit of time.

d. Lesion growth--the increase of lesion size per unit of time.

e. Infectious period--the period during which lesions sporulate.

These and other characteristics are well defined elements of epidemiologic theory as summarized in van der Plank's (1963, 1968) "mathematical model of resistance":

[1] *Authorities for Latin binomials are given in the proceedings subject index.*

$$\frac{dx_t}{dt} = R_c (x_{t-p} - x_{t-i-p}) (1 - x_t)$$

In this equation x_t is the proportion of susceptible tissue at time t, p is the latent period, i the infectious period, and R_c is the number of daughter lesions per mother lesion per unit of time. The epidemiological characteristics described could be called "components of resistance".

MONOCYCLIC TESTS

There are two types of resistance tests: "monocyclic" and "polycyclic". Cycle stands for infection cycle, the sequence of processes from one generation of spores through infection, latency, etc., to the next generation of spores. A single infection cycle from inoculation to resulting sporulation can be studied in detail under laboratory conditions. A test involving one infection cycle on one plant is called monocyclic.

Many laboratory investigations into the components of resistance are reviewed by Hooker (1967). The study of the infection ratio led to the finding of a stomatal exclusion mechanism against leaf rust (*Puccinia recondita*) of wheat (Romig and Caldwell, 1964). Differences in resistance of wheat to penetration of stem rust (*Puccinia graminis*) have been found (Brown and Shipton, 1964). Differences in latent period are obvious in potato late blight (*Phytophthora infestans*; Lapwood, 1961a) and stripe rust (yellow rust, *Puccinia striiformis*) of wheat (Zadoks, 1961). Differences in spore production have been found in *P. infestans* (Lapwood, 1961b; Van der Zaag, 1956) and in leaf rust of wheat (Zadoks, unpublished data). Usually, several components of resistance acting simultaneously determine overall resistance (Fig. 1).

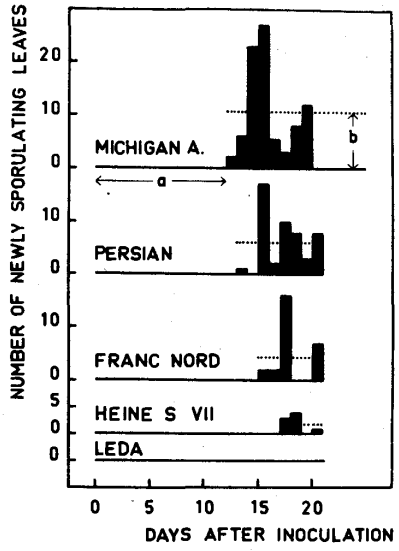


Figure 1. Components of resistance in five winter wheat cultivars inoculated with *Puccinia striiformis* race B7X in the field when the flag leaf was just visible; a = latent period, b = average infection ratio (after Zadoks, 1961, original data recalculated for 50 stems per cultivar).

For the purpose of comparison between different tests the most susceptible plant should be used as a susceptible control. For each character the disease rating of the test plant - DIS(T) - is expressed as a fraction of the disease rating of the susceptible control - DIS(S). Relative resistance RES is found by deducting this ratio from 1, i.e., by the formula

$$RES = 1 - \frac{DIS(T)}{DIS(S)} .$$

The data from measured components of resistance all can be included in a combined index of relative resistance (as in Table 1), which is again a value between zero and one.

Table 1. The combination of components of resistance into one index, the "relative resistance", in potato late blight (*Phytophthora infestans*). This index places the cultivars in the same ranking order as the official resistance rating based on numerous field observations (after van der Zaag, 1956, table 13)

Cultivar	Components of resistance DIS(T) with susceptibility =1			Product P	Relative resistance RES = 1 - P	Official resistance rating
	Infection lesion		sporulation rate			
	ratio	growth				
Eersteling DIS(S)	1.	1.	1.	1.	.000	.3
Eigenheimer	.4	.6	1.	.24	.760	.5
Voran	.2	.6	.2	.024	.976	.7
Noordeling	.2	.5	.15	.015	.985	.75

RUST NURSERIES

The components of resistance can be studied in the laboratory, but since laboratory tests are labor consuming they are usually bypassed in favor of field tests. A typical field test design is that of the rust "race nursery" (Fig. 2). Wheat cultivars are sown in clumps or short drills alongside a row of a highly susceptible cultivar. The latter, called a "spreader", is inoculated with one isolate. A localized but severe epidemic builds up and provides a gradually increasing amount of inoculum which spreads over the test cultivars. The resulting disease is assessed and a parameter of resistance calculated.

The epidemic as observed on a test cultivar is composite in origin. Part of the epidemic is due to the continuous influx of inoculum from the spreader and part due to inoculum produced by the test cultivar itself. Usually the spreader contributes most of the inoculum so that the epidemic observed on the test cultivar is a mere reflection of the epidemic on the spreader. In this case, the rust nursery test is little more than a "continuous monocyclic" test. This type of test underestimates the power of partial resistance.

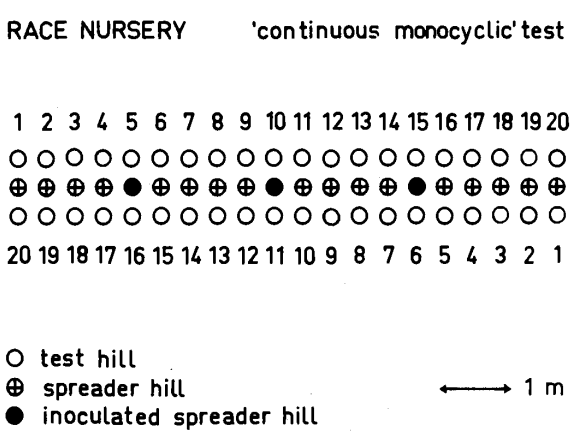


Figure 2. Design of a rust race nursery for monocyclic testing of resistance to one race of *Puccinia recondita* in 20 wheat cultivars. Cultivar clump diameter is 25 cm, distance between centers of clumps 40 cm (Zadoks, 1963).

POLYCYCLIC TESTS

Underestimation of the power of partial resistance is safe, but inefficient. The monocyclic test neglects the fact that an epidemic often builds up by successive infection cycles. Small differences in partial resistance as observed in a monocyclic test can have large effects after a number of repeating infection cycles. The monocyclic test is essentially an experiment with an individual plant. The polycyclic test is an experiment with a population of plants; it adds another dimension to disease resistance testing.

Field tests specially designed to evaluate the cumulative effects of partial resistance (Fig. 3), resemble small fields inoculated at the center. Amount and spread of the disease are assessed at regular intervals and parameters of susceptibility or resistance calculated accordingly. These tests reveal that some cultivars, highly susceptible according to their infection type, are"slow rusters" (Fig. 4). In slow rusters the epidemic builds up at a reduced rate and the resulting damage and yield losses are reduced accordingly (Romig, 1964).

It is not easy to combine accurate resistance tests with accurate yield tests, but many breeders have experienced that some cultivars yield better than others even when they have exactly the same level of disease (Clifford and Schafer, 1968). This phenomenon is called "tolerance" (Simons, 1966). Tolerance may be defined as resistance to damage. The genetics of tolerance are unknown and breeding for tolerance is only beginning to be practiced (Brönnimann, 1968).

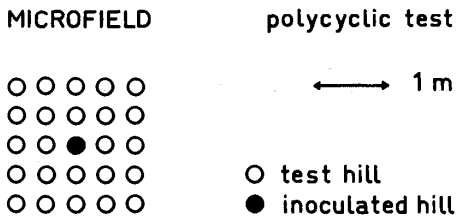


Figure 3. Design of a field experiment for polycyclic testing to estimate cumulative effects of partial resistance. A single *Puccinia recondita* isolate, inoculated on the central among 25 clumps of a single wheat cultivar, spreads over the population of host plants in successive infection cycles. Clump spacing as in Fig. 2.

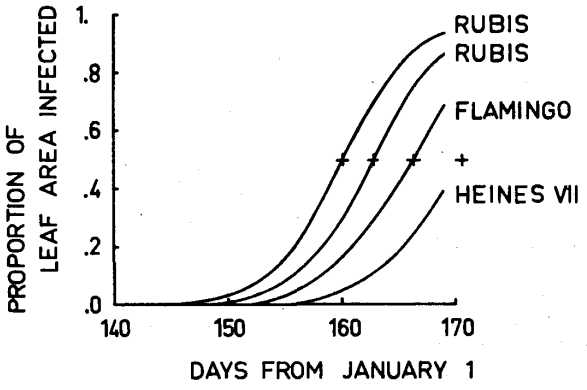


Figure 4. Demonstration of "slow rusting" in polycyclic tests. Four plots were established and inoculated as in Fig. 3, two of the plots containing the susceptible (control) cultivar Rubis, and the other two the widely-grown, slow rusting cultivars Heines VII and Flamingo. Differential rates of rust epidemic build-up are reflected in the differential slopes of the curves.

GENETICS OF RESISTANCE

RESISTANCE SPECTRA

Partial resistance is the result of the interaction between one test plant and one isolate of the pathogen. The test plant can be a representative of that population of nearly identical plants which is called a "cultivar". This cultivar can be a clonal line descending from one heterozygous hybrid (in potatoes) or a family of plants obtained by inbreeding from a single homozygous parent (in wheat). In a similar way, the pathogenic isolate can be representative of that group of isolates that is called a "physiologic race" because they have a combination of pathogenic characteristics not occurring in other isolates. In dealing with annual crops it is more precise to speak in terms of race-cultivar interaction than of isolate-test plant interaction.

A graphical representation of the "one race - one cultivar" interaction is given in Fig. 5. Resistance is depicted as a column with a height $0 \leq RES \leq 1$. The "one race - many cultivars" interaction is shown in Fig. 6 as a colonnade. The resulting picture is called an "infection spectrum". The picture of a "one cultivar - many races" interaction, shown in Fig. 7, may be called a "resistance spectrum". A cultivar showing high resistance to one and low resistance to another race differentiates between these two races and can be used as a "differential."

UNIFORM AND DIFFERENTIAL RESISTANCE

In some cases the resistance of the cultivar apparently is about equal to all races tested. Van der Plank calls this phenomenon "uniform resistance" (1969), a better term than his earlier "horizontal resistance" (1963; 1968). Uniform resistance may reach different levels (Fig. 8). In striking contrast with uniform resistance is "differential resistance", formerly called "vertical resistance" (van der Plank, 1968; 1969). The resistance spectrum can show all values for RES from 0 to 1. The best differentials for race identification are those which give either 0 or 1. Examples can be found in potato late blight (*P. infestans*) and flax rust (*M. lini*).

Typical uniform and typical differential resistance can occur together as van der Plank (1963) showed for the potato cultivars Kennebec and Maritta (Fig. 9) tested with *P. infestans*. This situation is called "two-dimensional resistance". In field tests with stripe rust (*P. striiformis*) of wheat, more complicated results were obtained which emphasize the hypothetical nature of the concept of horizontal resistance. Differential resistance can be recognized in cv. "Heines VII" but uniform resistance in its typical form is absent from both cv. Heines VII and cv. "Probus" (Fig. 10).

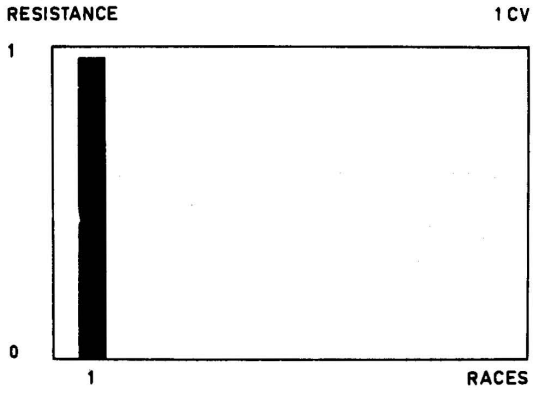


Figure 5. The "one race - one cultivar" interaction, with resistance nearly complete.

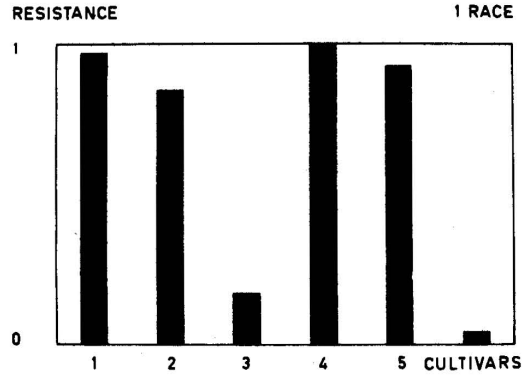


Figure 6. The "one race - many cultivars" interaction showing the "infection spectrum" (Zadoks, 1966) that indicates differential virulence.

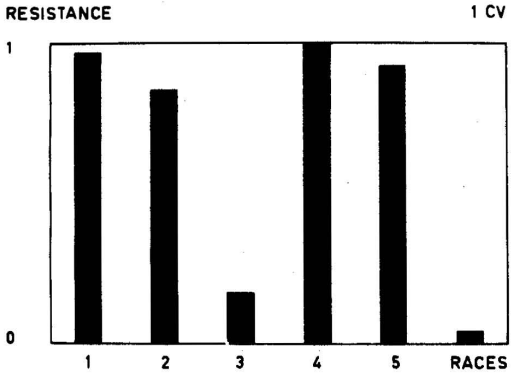


Figure 7. The "one cultivar - many races" interaction showing the "resistance spectrum" (Zadoks, 1966) typical for differential resistance.

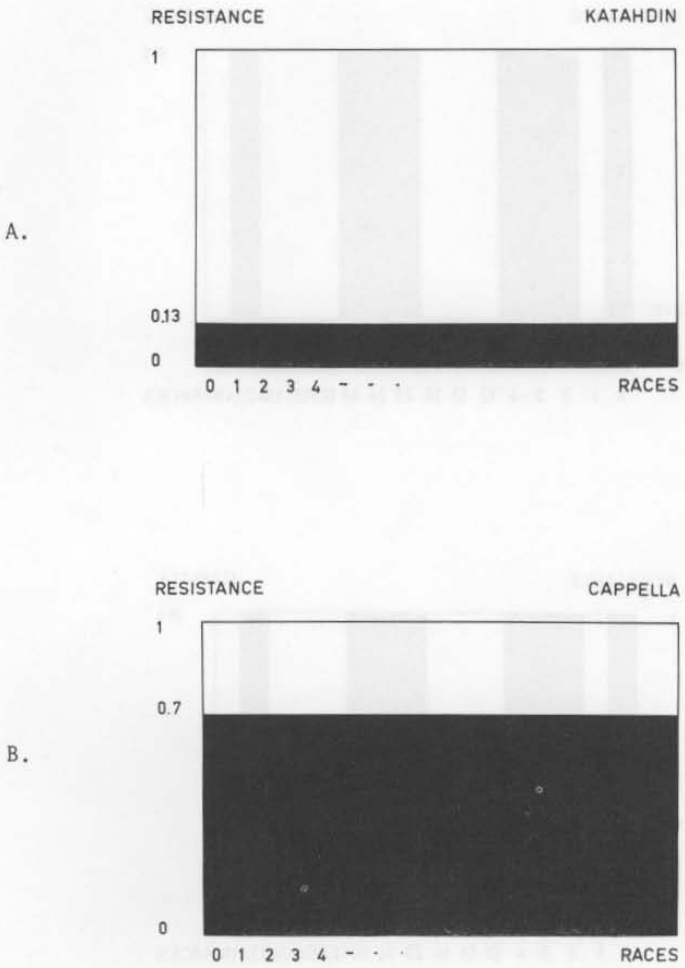
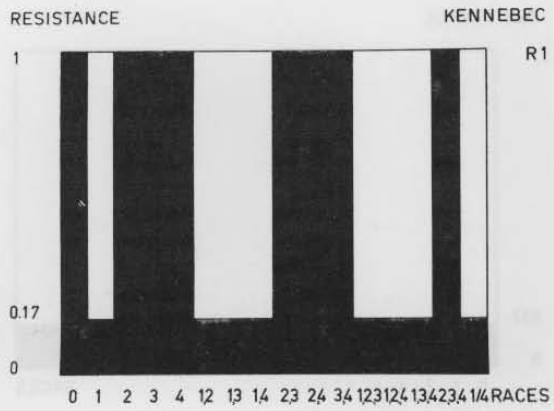


Figure 8. Uniform resistance at low (A) and high (B) levels, as demonstrated by resistance spectra for interactions of potato cultivars Katahdin and Capella with several races of *Phytophthora infestans* (after van der Plank, 1963).

A.



B.

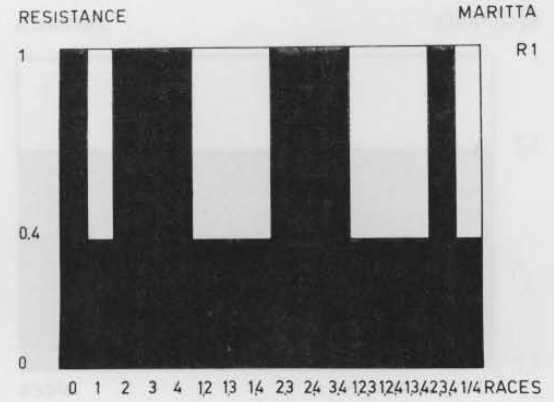


Figure 9. "Two-dimensional resistance" as demonstrated by the interactions of potato cultivars Kennebec (A), and Maritta (B), with *Phytophthora infestans*. Both cultivars carry the hypersensitivity monogene R1. This gene imparts complete, differential resistance to the races 0, 2, 3 and 4, and to the complex races 2,3; 2,4; 3,4; and 2,34 of the pathogen. Kennebec also displays a low, and Maritta a medium level of uniform resistance (after van der Plank, 1963).

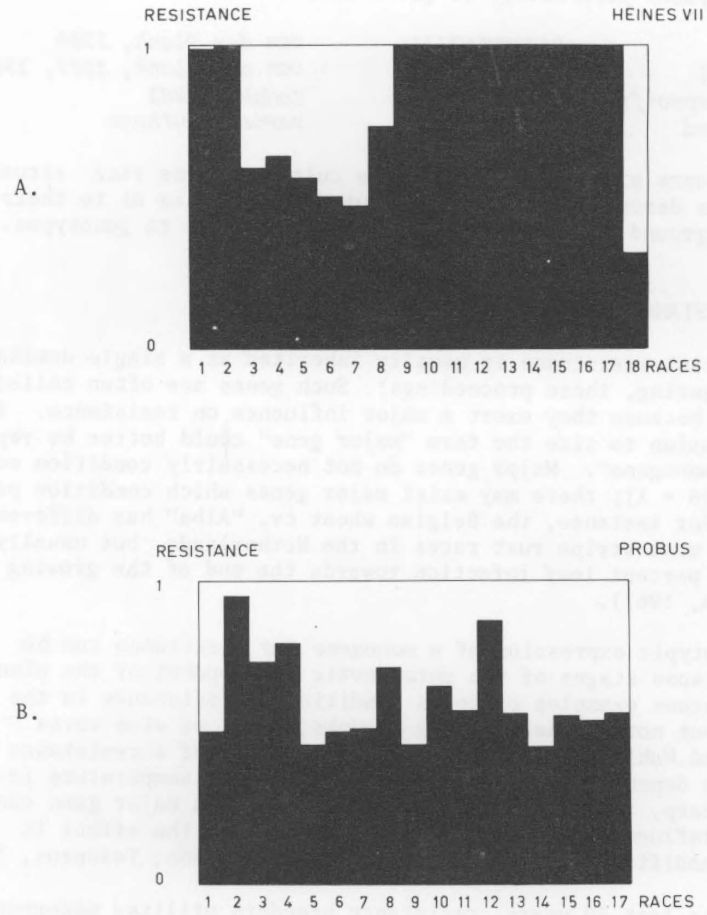


Figure 10. Interactions between winter wheat cultivars Heines VII (A) and Probus (B) and races of *Puccinia striiformis*. Heines VII displays high differential resistance apparently combined with moderate but quite irregular uniform resistance. With Probus, however, the resistance spectrum is difficult to interpret in terms of differential and uniform resistance (calculated from data of Stubbs, Vecht, and Fuchs, 1968).

To recapititulate the terminology, uniform, differential and two-dimensional resistance refer to the resistance spectrum as displayed under the one cultivar - many races situation. The preferred and the earlier, synonymous terminology is given below:

UNIFORM	*DIFFERENTIAL*	*van der Plank, 1969*
horizontal	*vertical*	*van der Plank, 1963, 1968*
race-non-specific	*race-specific*	*Zadoks, 1961*
generalized	*specific*	*various authors*

Partial resistance also refers to the one cultivar - one race situation. All these terms describe phenomena without any inference as to their genetical background; they refer to phenotypes but not to genotypes.

MONOGENIC RESISTANCE

Differential resistance is usually inherited as a single dominant gene (see Loegering, these proceedings). Such genes are often called "major" genes because they exert a major influence on resistance. To avoid any allusion to size the term "major gene" could better be replaced by the word "monogene". Major genes do not necessairly condition complete resistance (RES = 1); there may exist major genes which condition partial resistance. For instance, the Belgian wheat cv. "Alba" has differential resistance to most stripe rust races in the Netherlands, but usually shows 5 to 10 percent leaf infection towards the end of the growing season (Zadoks, 1961).

The phenotypic expression of a monogene for resistance can be suppressed in some stages of the ontogenetic development of the plant. There are numerous examples of genes conditioning resistance in the mature plant but not in the seedling (Zadoks, 1961) or vice versa (Sztejnberg and Wahl, 1967). Phenotypic expression of a resistance monogene often depends on environment, especially on temperature (e.g., Strobel and Sharp, 1965). The genic environment of a major gene can also have an influence on its phenotypic expression; the effect is ascribed to "modifier genes" (Knott and Anderson, 1956b; Toxopeus, 1958).

During the last 50 years, resistance breeders utilized monogenes because of the ease of handling (dominance) and the predictability of the results. Moreover, several monogenes can be brought together into one individual, the resulting resistance being called digenic, trigenic or oligogenic, respectively (van der Plank, 1968). Oligogenic resistance (genotype) is, as far as we know, always differential resistance (phenotype).

POLYGENIC RESISTANCE

Uniform resistance is supposed to have a different genetic basis. A great number of genes regulate the normal function of a plant. Many of these genes exert some effect on resistance. With respect to the criterium "resistance" these genes behave as "minor genes". Here, minor has the connotation of small in effect. When a minor gene can be identified by isolating its phenotypic effect from background noise it would become a major gene for partial resistance. To avoid the terminological problem van der Plank's (1968) term "polygene" is preferred. Polygenes exist even in the absence of the pathogen, apparently because their

other (metabolic) functions give them survival value. Thus their existence is not due to a differential selection pressure by a specific race of the pathogen. Polygenes have no differential effects; they convey uniform resistance. Polygenic resistance is a quantitative character and quantitative genetics should be applied in breeding for polygenic resistance.

The uniform resistance to *P. infestans* found in late maturing potato cultivars is often ascribed to "gene balance", a lucky combination of gametes with unpredictable inheritance. Toxopeus (1959) showed that transgression of (supposedly) uniform resistance occurred, some F_1 plants being more resistant to late blight than either parent. Hooker (1967, 1968), studying the adult plant resistance of maize against maize rust (*Puccinia sorghi*), determined the infection severity of individual plants in P, F_1, F_2 and F_3 populations. Inbred parents and F_1 populations were uniform; F_2 and F_3 populations showed much variation. The partial resistance of mature maize plants is polygenic, slightly dominant and highly heritable. Transgression of resistance was not unusual. So-called minor genes for resistance against stripe rust in wheat seem to be additive in effect (Lewellen and Sharp, 1968).

ENVIRONMENT AND DISEASE EXPRESSION

Monogenic qualitative inheritance and polygenic quantitative inheritance have been represented as two contrasting systems. The data presented on stripe rust of wheat in the Netherlands suggest that the contrast should not be stressed too much. It is better to regard these two systems of inheritance as extremes of a wide range of possibilities.

Detailed investigations into cotton blight, caused by the bacterium *Xanthomonas malvacearum*, illustrate that the host-parasite relationship is a dynamic system in which disease expression depends on the interaction (in the statistical sense) of environment with the genetic systems of host and pathogen. A population which is uniform in disease expression in one environment can show a great variability under another set of environmental conditions. In the latter case types could be selected resistant in both environments (Arnold and Brown, 1968). The magnitude of the gene effects, reflected in the terms "minor" and "major" gene, can be a function of environment. What seems to be a monogenic system in one environment may appear as a polygenic system in another environment. A concept like gene penetrance bridges the apparent discrepancy.

RESISTANCE BREEDING

In annual crops, the breeding for high resistance conditioned by one or a few genes often follows a simple scheme. A resistant parent is crossed with a susceptible parent of high agricultural value. The resulting hybrid is resistant but contains unwanted germ plasm from the resistant parent. This is eliminated by repeated backcrossing to the agronomically valuable parent. The plants of the successive daughter generations are exposed to infection and all susceptible plants rejected.

Tactics in breeding for uniform resistance are being developed in recent years. Among the selection criteria used by the breeder are the infection ratio (Umaerus, 1968) and the latent period (Rudorf and Schaper, 1954). The infectious period is difficult to measure and,

therefore, less suitable as a criterium. The sporulation rate is easily measured and it may be a valuable criterium. The epidemiologist considers these components of resistance, especially infection ratio, latent period and sporulation rate, as suitable selection criteria. Information on the heritability of these components of resistance is, unfortunately, scarce.

EPIDEMIOLOGICAL CONSEQUENCE OF BREEDING TACTICS

Breeding tactics have epidemiological consequences. There is evidence that the potato cultivars used in Europe around 1845, when *Phytophthora infestans* first spread over the continent, were much more susceptible than the cultivars grown later, in the intervening period before the introduction of differential resistance. In the interim farmers reaped the fruits of natural selection for partial resistance, now thought to be uniform (van der Plank, 1963).

A more recent example comes from maize. Tropical maize rust, *Puccinia polysora*, was first introduced into Africa in the late 1940's. After a few years of severe losses the local maize populations recovered and tropical maize rust is no longer a major threat. Again, natural selection produced an adequate partial resistance, probably uniform and of polygenic inheritance (van der Plank, 1968).

In the corn belt of the U.S., the other maize rust, *P. sorghi*, is more prevalent. Many races of this rust are known but nevertheless known genes for differential resistance are not commonly used in breeding programs. The partial but uniform resistance obtained without much conscious effort is satisfactory.

The story of differential resistance is in dramatic contrast to the tale of uniform resistance. Differential resistance was first used around 1920 to control diseases like stem rust of wheat (*P. graminis*) and late blight of potatoes (*P. infestans*). Unfortunately, the pathogens showed a remarkable adaptability. Disease-free crops carrying the new resistance genes provided an ideal medium for the selection of genes for differential virulence in the pathogens. The result was a race between breeder and pathogen, the breeder producing new cultivars carrying new differential genes for resistance and the pathogen adapting itself time and again by producing the compatible genes for differential virulence. The average useful life of wheat cultivars in Mexico is about five years because of stem rust (Borlaug, 1965). The same is approximately true in the Netherlands where the appearance of new stripe rust races (*P. striiformis*) in commercial wheat fields has a frequency of nearly one per year.

Most of the differential resistance genes used are dominant and therefore epistatic to the polygenes conditioning uniform resistance. Effects of the polygenes for resistance are masked, and as a consequence they are diluted in successive breeding cycles until uniform resistance is lost. This phenomenon is known as the "Vertifolia effect" (van der Plank, 1963). The Vertifolia effect is dangerous because the uniform resistance can serve as a second line of defense when the first line of defense, differential resistance, has been broken. In the pathogen, differential genes for virulence characterize the physiological races as the breeder knows them. They are produced by mutation, they are combined and recombined by sexual or parasexual processes, and they are selected

because of their survival value. They have survival value in host populations with differential genes for resistance, but there is ample evidence that they have a selective disadvantage in the absence of differential host resistance.

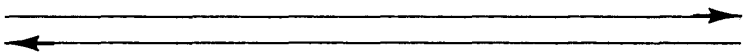
These considerations led van der Plank (1968) to his theorem of "homeostasis" diagrammed below:

HOMEOSTASIS

Susceptible hosts *Resistant hosts*

Directional selection

(Selection for virulence)



Stabilizing selection

(Directional selection pressure removed)

When the pathogen population is presented with differentially resistant hosts instead of susceptible ones, directional selection for virulence will take place. The reverse change is effectuated by stabilizing selection when the differentially resistant hosts are removed. From: van der Plank, 1968.

Directional selection for differential virulence by differentially resistant hosts is balanced by the stabilizing selection due to decreased fitness associated with differential virulence. In typically biotrophic pathogens like rust the directional selection can be strong; in pathogens with an important non-parasitic phase stabilizing selection is strong.

TOWARDS A STRATEGY

PREMISES

A strategy against blister rust (pathogen *Cronartium ribicola*) of western white pine (*Pinus monticola*), to concentrate on this particular problem, has to be mapped out. The premises are:

1. There is a fair degree of intraspecific variability in western white pine (Ahlgren, 1968; Bingham, 1966).

2. In the western white pine area there exists a great variety of environmental conditions.

3. *Ribes* species, serving as alternate hosts of the rust, cannot be eradicated completely (Peterson and Jewell, 1968).

4. Physiologic races characterized by differential genes for virulence are not yet known in *Cronartium ribicola* (Ahlgren, 1968; Peterson and Jewell, 1968).[2]

From an evolutionary point of view, the stable ecosystem of western white pine has been unbalanced by the introduction of blister rust. The time needed to restore equilibrium is called "relaxation period". A rough guess for this relaxation period is five to ten generations. In evolutionary perspective the strategic problem is far from hopeless. With the possible exception of the chestnut (*Castanea dentata*) destroyed by the chestnut blight (*Endothia parasitica*) nature solves its own problems through the action of quantitative genetics. But nobody can wait for the natural solution which takes five to ten generations or about half a milienium.

MONOGENIC RESISTANCE

Monogenic resistance tends to be self-destructive (Person, 1966). The sequence of differential resistance over differential selection to differential virulence which destroys the original resistance has the character of a "boomerang effect". Wheat and potatoes can be harvested before the boomerang hits, pine trees probably cannot.

Wheat breeders tried many tricks to lessen the boomerang effect. One is to incorporate several different monogenes for resistance in one cultivar. The trick seems too laborious for application in tree breeding; moreover it does not work too well. The pathogen can collect the compatible set of virulence genes in one physiologic race. Among the examples, too numerous for citation, is one of a tree rust, a leaf rust of coffee (*Hemileia vastatrix*; Noronha-Wagner and Bettencourt, 1967).

A second trick, advocated by Borlaug (1959, 1965), is the composite cultivar. Wheat lines are bred differing from each other in one monogene for resistance but identical in all other respects. Seed from different lines is mixed to sow a wheat crop that is uniform in agronomical characters but composite with respect to resistance. The trick uses a polycyclic effect and works well when a rust population builds up gradually (Table 2). However, in western white pine blister rust polycyclic effects are of little importance and the trick is spoiled where presence of *Ribes* spp. permits an unrestricted multiplication of inoculum.

[2] *Editors note: Later in the symposium (cf. Hoff and McDonald, these proceedings) it was stated, on the basis of unpublished data, that at least two pathogenic races of* C. ribicola *exist.*

Table 2. Composite design applied to stripe rust (*Puccinia striiformis*) in winter wheat

Cultivar	Disease severity (fraction of leaf area diseased) [a]
Heines VII	0.105
1 to 1 mixture	0.013
Panter	0.000

[a] *The Netherlands, 1958, unreplicated plots, plot size 1 ha, natural infection, weather not very favorable to rust.*

A third trick has been proposed by several authors (see Johnson, 1958). The host area is divided into sub-areas, every sub-area being protected by another monogene. In this way, a mosaic of resistance genes is created. In the North-West-European wheat belt, a comparable situation was unconsciously created by national regulations; sometimes the trick was effective (Zadoks, 1961).

In this rather gloomy perspective for differential resistance there is one spark of light. The epidemiological system under consideration is a host-host-pathogen system (van der Plank, 1968), or more precisely a *Pinus-Ribes-Cronartium* system. Differential selection in the pine phase will possibly be counter-balanced by stabilizing selection in the ribes phase.

POLYGENIC RESISTANCE

When man wants to speed up the work that nature does too slowly, the conscious exploitation of intraspecific variations in resistance seems the most promising way. The system uses well adapted parents and does not introduce unwanted germ plasm. However, full resistance is difficult to obtain within a few generations(Bingham, 1966). Therefore it is necessary to establish accurately what level of partial resistance is acceptable. The purpose of this type of breeding is not to eliminate the rust, but to live with it.

The ecosystem of blister rust on western white pine is not only a host-host-pathogen system but also an environment-host-pathogen-system. The environment-pathogen relation has been studied extensively. The results indicate the existence of danger areas, where the rust readily infects the pine, and of fringe areas, where the frequency of infection is reduced because of specific ecological conditions (Paterson and Jewell, 1968; Van Arsdel, these proceedings.

The environment-host-pathogen system has been little studied. For example it is known that in colder areas the latent period of the rust is prolonged, but this is little more than an environment-pathogen relation. The studies proposed here are investigations on the interactions between environment, host genome and rust genome. Results of this type

of study could indicate a particular genotype of the pine ensuring partial resistance which is inadequate in one environment but significantly better and economically valuable in another environment. If such interactions between resistance and environment exist, they must be discovered and utilized. To study this aspect a close cooperation is needed between epidemiologists, ecologists and breeders.

CONCLUSIONS ON THE USE OF MONO- AND POLYGENIC RESISTANCE

1. When differential resistance is used specially adapted physiologic races can appear. Theoretically the risk is small, but the economical consequences are too big to ignore this risk.

2. Two precautions may reduce the economical effects when the risk materializes, though the first one is considered to be of relatively little value:

   a. mixed planting of trees from different genetic stocks ("composite design"), and

   b. planting different areas with populations of different descent ("mosaic design").

3. The use of polygenes in breeding for partial resistance is "nature's own method" and it is possibly the fastest and safest way to improvement.

4. Environment-host-pathogen interactions should be investigated and, when possible, utilized.

REFLECTIONS

The perfect breeding system does not exist. The search for monogenes has to be continued and those tricks which can prolong the life expectancy of monogenes must be tried. At the same time the theory of quantitative genetics should be applied to partial resistance, with due respect for genotype-environment interactions.

Most important is that all objectives are specified explicitly and executed according to specifications, the long term acquisition of data on the results being part of the specifications. The information collected should be examined regularly and without prejudice. Reforestation of big areas is a lengthy process; every year the next move can be planned in due consideration of the accumulating information.

In an attempt to formulate possible research and breeding objectives the author left the realm of facts and ventured into the fringe zones of wishful thinking. Maybe he lost his way. Maybe there are many ways towards pine rust control. These, however, have to be traced and paved by those who are on the job.

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FLOOR DISCUSSION

BINGHAM: I think one of the most helpful suggestions you may have made to us was the possibility of selection for long-lasting "uniform" resistance, usually expressed quantitatively. In respect to selecting for uniform resistance to *C. ribicola*, among other selection criteria perhaps useful might be things you suggested like low infection ratio, or prolonged latent period. It is easy to foresee how we might select for low infection ratio--merely by selecting plants with fewer foliar or bark lesions per unit area of host infection court. But how we might benefit from selecting for a prolonged latent period, with the rust perhaps fruiting a year later (as actually noted by Van Vloten in the Netherlands, and much earlier by Eriksson in Sweden), escapes me. Aecial sporulation in certain *P. strobus* provenances was delayed, I believe up to a full year, but thereafter bark lesion development was normal and the trees all died. Would you care to comment on how selection for lengthened latent period might be useful in selection for resistance to cronartium rusts?

ZADOKS: Of course your situation with cronartium rusts is quite different from that encountered in rusts of annual crops. In annual crops one rust lesion does not kill the plant; with pines, one stem lesion usually does. So latent periods may not be a very helpful selection criterion, unless linked with other more valuable criteria. I don't know whether there is a real, genetic linkage. More often than not, however, a prolonged latent period reduces the rust population build up rate in annual plants. Even though a prolonged latent period may not seem to have much value for you, it's a fairly easy criterion to select for, and it may be linked with more valuable criteria.

QUESTIONS OF RACE DIFFERENTIATION WORK IN CEREAL RUSTS

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ABSTRACT

Out of practical work with physiologic races of the stripe rust of wheat and barley (*Puccinia striiformis*) some general and some especial aspects of differentiation and description will be discussed.

Race determination in cereal rusts is based on differential varieties of the uredo-host, tested under more or less controlled conditions, and distinguished by different infection types of the host-pathogen-system.

The detection and the replacement of differential varieties has a long history and has during years and a generation of scientists shifted from empirically identified differentiating varieties to genetically labeled ones.

Three main groups of differential varieties are generally employed: main differentials, additional differentials and screening varieties.

The question of internationality of differential sets will be touched.

Host and pathogen are very much dependent on the environmental conditions. Many efforts have been made to standardize the growth conditions of both and to reach reliable and reproducible results.

In certain cases the determination of physiologic races, in the seedling stage of the host, under the rather artificial conditions holding in greenhouse and growth chamber is not sufficient. The facts (1) that the seedling cereal plant generally is more susceptible than the same plant in the later stages of development, and (2) that the plant throughout its various growth stages is able to show wider differentiation of rust infection (both in type and degree), together with numerous observations with the same set of varieties in different places and different years. has led to the description of "field races".

Some additional characteristics in race determination can be the differences in "transfer-time", the differences in optimal temperatures, and the differences in germ tube development of the spores.

Race classification or taxonomy is in a constant state of flux. Practical breeding objectives, which may change at any time, have to be combined with internationality or universality in this "small world".

INTRODUCTION

To begin with the truth, I am just an old fashioned, patient (too patient, perhaps), practical determinator of races of stripe rust of wheat (*Puccinia striiformis* West.), working mainly with seedling plants in the first leaf stage. I am going to show you an everyday struggle with the business of determining physiologic races of stripe rust. In doing this I should give you a brief introduction to this host-parasite couple. We are dealing with an annual host (exhibiting a great deal of variability grown under conditions that allow rapid changing of varieties). Also, the alternate host for *P. striiformis* is unknown. Both points are different from your problems with tree rusts, but there should be some room for comparison.

Race determination in cereal rusts is generally based on differential varieties of the uredial host tested under more or less controlled conditions and distinguished by different "infection types" of the host-parasite system. The infection types of the wheat-stripe rust system have been defined as follows:

i	= immune, no kind of fleck or pustule visible
i-0	= some light chlorotic flecks ("oo" with other authors)
0	= chlorosis and necrosis, no pustules
I	= chlorosis and necrosis, very few and very small pustules
II	= chlorosis, less necrosis, few pustules, small to medium size
III	= chlorosis, abundant pustules of normal (susceptible) size
IV	= no chlorosis, abundant normal pustules

My work with this host-parasite system has led me to make three generalizations about determination of rust races. First, the discovery of a good differential variety is mainly luck. Second, a list of races is an agreement (convention), and third, the practicability of a race list is a kind of historical question.

DIFFERENTIAL VARIETIES

Physiologic races were first detected (and still will be) when one variety was highly infected in one region but not in the other, while a second variety reacted in an opposite manner. "Region" may be area or time. All classical differential sets started this way. Later on they were refined, enlarged, and sometimes diminished again. With the first ecstasy of discovery Gassner and Straib (1932) described 14 races with 10 differentials. When Straib left Braunschweig in 1945 he had defined 54 races using 11 differentials. After 14 years on the job, I could not agree that some of the original differentials were of value. So, I combined some races which showed differences only on the unreliable differential varieties (Fuchs, 1960, 1965).

Manners (1950) in his yellow rust work came to the same conclusions pronouncing "Stakman's rule" (Stakman, 1947) that a new "physiologic race of rust must not be established unless there is a consistent difference in reaction type on one or more hosts at least as great as that between susceptible and mesothetic, or between mesothetic and resistant." The list of races of the other cereal rusts, which have an alternate host and which are far more investigated, are much longer, like the list of stem rust races of wheat with 297 races in 1962 (Stakman, Stewart, and Loegering, 1962).

New epidemics on hitherto resistant varieties very often create a new differential. For example, the varieties Cleo, Falco, and Opal were not infected with race 3/55 until 1960 and have remained susceptible (Ubels, Stubbs, and s'Jacob, 1965). Unfortunately Cleo and Falco are not seedling differentials, since reactions on seedlings do not distinguish between 0 and IV infection types. The same is true for the famous Heine VII, which has a rather distinguished stripe rust response in the field but not in the greenhouse in seedling stage plants (Fuchs, 1960). The variety Opal seems to be a much better possibility of a new differential variety both in the field and in the house.

Another example of the creation of a new differential and, at the same time, a new race happened in the United Kingdom and the Netherlands in 1965 (Macer and Doling, 1966; Fuchs, 1967), and gives another illustration for the race between breeder and fungus in nature. The variety Rothwell Perdix had shown excellent resistance against the main northern European races 3/55, 8, 27/53, and 54. When planted to a larger extent, however, it showed a stripe rust infection that has increased every year since then (only last year it seemed to stop spreading to other countries).

In Table 1 you will find the main European stripe rust races characterized by their behaviour on some differential wheat varieties, both in the field and on the seedling stage in the greenhouse. Michigan Amber is the generally susceptible host, highly infected with all races. Vilmorin 23 and Cappelle are susceptible to the 3/55 race but resistant to all other races mentioned here. Chinese 166 is susceptible to 27/53 and 60 races, and Heines Kolben is susceptible to 54 and 60 races. Rothwell Perdix was resistant to all the older races, but was susceptible to the new race 60. Heine VII exhibited uniform susceptibility in the seedling stage in the greenhouse, but showed differential resistance when mature plants were tested in the field.

If Opal were brought into this system, it would show its "additional differential" character, allowing a subdivision in the race 3/55 group, while Rothwell Perdix has an independent "main differential" character.

People working with differentials of variable reliability are always happy to meet good additional or supporting differentials. I started to search for a good additional differential myself, by testing in the greenhouse hundreds of varieties that promised some hope for this purpose. Four groups were defined as follows:

(1) generally susceptible (the main amount),

(2) differentiating to some extent, but not very reliable (rather small amount),

Table 1. Behavior of principal European races of stripe rust in the field and greenhouse on some differential varieties of wheat

Variety	Races									
	3/55		8		27/53		54		60	
	Field	House	Field	House	Field	House	Field	House	Field	House
Vilmorin 23	+++	IV	0	0	0	0	0	0	0	0-IV
Cappelle	++	0-IV	0	0	0	0	0	0	0	0+
Heine VII	0	0-IV	+++	IV-	0	0-IV	+++	IV	+++	IV-
Chinese 166	0	0	0	0	+++	IV	0	0	+++	IV
Heines Kolben	0	0	0	0	0	0	+++	IV	+++	IV
Heines Peko	0	0	0	0	0	0	+++	0-IV	++	0-IV
Rothwell Perdix	0	0	0	0	0	0	0	0	+++	IV
Michigan Amber	+++	IV	+++	IV	+++	IV	+++	IV	+++	IV

Degree of field infection: + = low; ++ = medium high; +++ = high.

(3) differentiating and useful (a very few), and

(4) generally resistant (a few).

In groups (2) and (3) only one really new differential variety group has been found during 7 years of testing, i.e., nearly all varieties differentiating at all reacted like the already known differentials, although at different intensities. Cappele and Heines Peko in Table 1 are additional differentials. The varieties in Table 2 show a decreasing line of clear infection types (Fuchs, 1966).

Table 2. Supporting differentials used for race determination based on seedling reaction types

Variety	Race 3/55	Race 54	Race 20A
Vilmorin 23	IV	0	i-0
Nord Desprez	IV-	0	i-0
Cappelle Desprez	0-IV	i-0	i
Heines Kolben	0	IV	II
Heines Peko	i-0	II-IV	0
Lee	0	0	IV
Reichersberg 42	0	0	0-IV

I have to give an explanation to the note "0-IV", which looks like nonsense. The wheat variety-stripe rust system is sensitive to all kinds of environmental influences. I will discuss this point later. The additional differentials like Cappelle and Heines Kolben don't always give reproducible results. Still they serve in determinations to some extent, since this variability seems to be under genetic control. Sometimes there are different infection types on plants in one test pot, so that the reading "0-IV" means a variation under absolutely equal conditions.

An explanation to the type "i-0" is also called for. Very often these supporting differentials show less definite infection types than the main differentials do in the same replication.

It is up to you to decide if a variety is to be a differential or not, and concurrently how many races you are going to nominate. This process of looking for differentials and reassuring the results never will stop, combined of course with a strong selection of the differential variety seed. But what about practical importance and necessity. The race determination that we do in Europe may be of little value to other areas. Fourteen years ago the Netherlands Grain Center started a European yellow rust trial which still is working for Europe and other areas as well. At Braunschweig, Germany, we try to identify the physiologic races in the stripe rust samples sent from these trials. Through

the years we became aware of a race group (20A) occurring on Mediterranean samples. Since this race group was a problem in the Mediterranean, a differentiation was necessary. Utilization of a variety believed to be resistant to race group 20A provided the differentiation. Local varieties or varieties from neighboring countries should be tested intensively.

Names and numbers of races don't say anything, if they are not connected with applied genetical knowledge. Last year we received many samples from Israel and by luck we were able to find three different races within the 20A race group by using the "resistant" wheat P.I. 178 383, which is a very important parent in stripe rust resistance breeding in the U.S.A. (Sharp and Hehn, 1967), and the "supporting differential" Reichersberg 42 which gave a clearer reaction than usual. The differentiation of race 20A is shown in Table 3.

Table 3. Differentiation of Race 20A of stripe rust into 3 races by use of seedling reaction of supporting differentials

Varieties	Race 20A		
	Variation 1	Variation 2	Variation 3
Heines Kolben	IV	II-	0+
Reichersberg 42	0	IV	0
P. I. 178 383	i-0	i-0	IV
Lee[a]	IV	IV	IV

[a]Race 20A is characterized by virulence for the differential Lee and some virulence for the differential Heines Kolben.

FIELD RACES

Now it is time to switch over to the field races, described by Zadoks (1961, 1963) and Ubels, Stubbs and s'Jacob (1965). Plants in the seedling stage very often are more highly susceptible than in later stages of development, and the adult plant is able to show more differentiation of rust infection (type and degree) than the young one. Based on field infection data from all over Europe, Zadoks concluded that field races could be defined. Ubels, Stubbs, and s'Jacob (1965) provided the following interpretation of their results. Flamingo race and Peko race, both defined as race 54 in the greenhouse, have a distinct difference in the field race trials. Leda race and Heine VII race, both in the race 8 group, show differences on Leda. Somewhat exciting was the Cleo race, which infected Heine VII and some other varieties in the field, and gave the race 3/55 picture in the greenhouse tests.

Concerning the varieties themselves, each seems to have its own race infecting it to a higher degree than the other races would.

So, in certain cases, field observations and experiments in isolated field plots split up the race determination done in the greenhouse. We

decided that a race determination in stripe rust should combine both the field observations and the greenhouse tests.

Summarizing this section on differential varieties one can name three groups of varieties:

(1) main differentials (good, proved, universally useful differential varieties),

(2) supporting differentials (fairly good varieties, which react parallel to the main differentials but with slight differences, which one day may help to find real differences), and

(3) resistant varieties (varieties, so far resistant to all known races, which one day--if susceptible--will immediately show the occurrence of a new race).

Nearly all cereal rust race workers dealing with cereal rust have such sets. But there is the modern story about differentials which Dr. Loegering, one of the leading scientists in this field, has already treated in his paper presented at this symposium. This work was mainly done with stem rust of wheat (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn.), and less intensively with stripe rust of wheat. Nevertheless there is some literature on genetic analysis of differential varieties and the efforts to come to single factor lines for stripe rust race determination (Macer, 1966; Allan and Purdy, 1967; Lewellen and Sharp, 1968; Brown and Sharp, 1969) in recent years.

The publications quoted last discuss the dependence of susceptibility and resistance reactions on the change in the night-day temperature profiles, leading to the description of "major" and "minor" genes (Sharp and Hehn, 1967), as reported and commented on by Dr. Zadoks in this symposium. One of the demands of Brown and Sharp (1969) is: "researchers working with physiologic race identification in *Puccinia striiformis tritici* should avoid use of varieties containing minor recessive genes if at all possible."

ENVIRONMENTS

In the everyday struggle of a race determinator, all factors do their best to complicate reproducible results in race determination. Environmental effects are well known. The influence of light, humidity, temperature, and nutrition on the different stages of host and pathogen development is described in many papers, and will have to be studied for every host-parasite system, probably in every locality.

In modern institutions, climate rooms and growth chambers are available and allow standardizing of the methods and should help both cultivation and testing. In our institute, Hille (unpublished) developed a small growth chamber where he was very successful in growing some races of stripe rust. Then we started combined experiments in these growth chambers and in the greenhouse to compare the infection type reactions of some races on some differentials. I expected the good differentials would react the same in both systems, since they had worked very well in the climate greenhouse with its relatively unsteady conditions, and that unstable or bad differentials would exhibit clear variation in reaction types in the growth chambers. Here are some of the results.

The behaviour of the differential Chinese 166 (Table 4) is rather clear cut as shown by the Lit. column. The reaction is either resistant (i-0) or susceptible (II-IV). However, there is some uncertainty (0-IV) under growth chamber conditions in the higher temperature profile (22) for race 27/53.

Table 4. Seedling reaction of wheat variety Chinese 166 to 13 races of stripe rust under differing environmental conditions

	Conditions				
Race	Lit.[a]	22/16[b] 3000	22/16[b] 1000	17/13[b] 3000	Green house[c]
60	IV	IV-	0-IV	IV	IV
1	i-0	i-0	i-0	i-0	i-0
54	0	i-0	i-0	i-0	i-0
42A	IV	IV	IV	IV	IV
20A	0	i-0	i-0	i-0	i-0
27/53	II-IV	0-IV	0-II	IV-	IV-
2	i-0	i-0	i-0	i-0	i-0
3/55	i-0	i-0	i-0	i-0	i-0
32A	i-0	i-0	i-0	i-0	i-0
32	i-0	i-0	i-0	i-0	i-0
26	i-0	i-0	i-0	i-0	i-0
7	i-0	i-0	i-0	i-0	i-0
15	i-0	i-0	i-0	i-0	i-0

[a] Indicates the combined results of thousands of greenhouse tests, as reported in the literature.

[b] Temperatures in degrees C/photoperiod in hours; light intensity in lux.

[c] Temperature 17°C±2°; light intensity 4000 up to 14,000 lux.

Heines Kolben (Table 5) is a good main differential variety, so that the mesothetic type reaction (II±) should be trusted. It is possibly the best example of a good differential I could show you now. The development of the uncertain reaction (0-IV) should be noted for race 42A.

Table 5. Seedling reaction of wheat variety Heines Kolben to 13 races of stripe rust under differing environmental conditions

	Conditions				
Race	Lit.[a]	22/16[b] 3000	22/16[b] 1000	17/13[b] 3000	Green-house[c]
60	IV	IV	IV	IV	IV
1	IV	IV	IV	IV	IV
54	IV	IV	IV	IV	IV
42A	II+	0-II	0-IV	0-II	0-IV
20A	II+	0+	0-IV	0-II	0
27/53	0	0	0	0	0
2	0	0	0	0	i-0
3/35	0	0	0	0	i-0
32A	0	0	0	0	0
32	0	0	0	0	0
26	0	0	0	0	0
7	0	0	0	0	i-0
15	0	0	0	0	0

[a] Indicates the combined results of thousands of greenhouse tests.

[b] Temperature in degrees C/photoperiod in hours; light intensity in lux.

[c] Temperature 17°C±2°; light intensity 4000 up to 14,000 lux.

Vilmorin 23 (Table 6) used to be a very good differential with clear cut 0 for resistance, IV for susceptibility and 0+ to II+ as a mesothetic type with some races. As you can see, it didn't work through the growth chambers (races 54, 60, 26, 7 and 15). But the mesothetic type reaction for races 32 and 32A was valid through all conditions.

Table 6. Seedling reaction of wheat variety Vilmorin 23 to 13 races of stripe rust under differing environmental conditions

Race	Conditions				
	Lit.[a]	22/16[b] 3000	22/16[b] 1000	17/13[b] 3000	Green-house[c]
60	0+	IV	IV	0-IV	0
1	IV	IV	IV	IV	IV
54	0	IV	IV	0+	0
42A	0	0+	0+	0+	0
20A	0	0+	0	0+	0
27/53	0	0	0+	0	0
2	IV	IV	IV	IV	IV
3/55	IV	IV	IV	IV	IV
32A	II+	II-IV	II-IV	II-IV	0-IV
32	II+	II-IV	II-IV	0-IV	0+
26	0	0	0-IV	--	0
7	0	II	0+	--	0
15	0	0	0-IV	0	0

[a] Indicates the combined results of thousands of greenhouse tests.

[b] Temperature in degrees C/photoperiod in hours; light intensity in lux.

[c] Temperature 17°C±2°; light intensity 4000 up to 14,000 lux.

With Lee (Table 7) the clear cut differences of the greenhouse disappeared nearly everywhere.

Spaldings prolific (Table 8) was known to be a rather bad differential, but if the reaction observed was exactly resistant (as with races 1, 42A, 20A) or if it was exactly susceptible (as with races 2, 26, 15) the variety was useful. This differential exhibited little variation under the conditions of this experiment.

Table 7. Seedling reaction of wheat variety Lee to 13 races of stripe rust under differing environmental conditions

	Conditions				
Race	Lit.[a]	22/16[b] 3000	22/16[b] 1000	17/13[b] 3000	Green-house[c]
60	0	II	0+	0-II	0
1	0	0-II	II-IV	0	0
54	0	0-II	II-IV	0+	0
42A	IV	IV	IV	IV	IV
20A	IV	IV	IV	IV	IV
27/53	0	II-IV	0-II	0-II	0+
2	0	0	II-	0	0(+)
3/55	0	II-	0-IV	0+	0
32A	IV	IV	IV	IV	IV
32	0	II-IV	II-IV	0+	0(+)
26	0	0	II-IV	0	0
7	0	II-	0-IV	--	0+
15	0	0	0-IV	0	0(+)

[a] Indicates the combined results of thousands of greenhouse tests.

[b] Temperature in degrees C/photoperiod in hours; light intensity in lux.

[c] Temperature 17°C±2°; light intensity 4000 up to 14,000 lux.

We see that environmental factors must also be controlled if differential variations are to give reproducible results.

Person, Samborski, and Forsyth (1957) reported on the use of detached leaves for race differentiation. In spite of good results in mildew race identification (Wolfe, 1967; Plate and Fischbeck, 1969) cereal rust investigators have dropped this method since susceptibility was much higher in detached leaves than in leaves in their natural connection with the plant (Browder, 1964; Samborski, Forsyth, and Person, 1958).

Table 8. Seedling reaction of wheat variety Spalding's prolific to races of stripe rust under differing environmental conditions

Race	Conditions				
	Lit.[a]	22/16[b] 3000	22/16[b] 1000	17/13[b] 3000	Green-house[c]
60	0-IV	II-	0-IV	0	0+
1	i	i-0	0+	i	i
54	0+	0-IV	0-IV	0	0+
42A	i	i-0	i-0	i-0	i
20A	i-0	i-0	i-0	i	i
27/53	0+	II-IV	II-IV	0	0
2	IV	IV	IV	IV-	IV-
3/55	i-0+	0	i-0	i-0	i
32A	0-IV	ii-IV	IV-	0-II	0-IV
32	0-IV	IV	IV	IV	IV
26	IV	IV	IV	IV	IV
7	0+	II+	0-IV	0-IV	0
15	IV	IV	IV	IV	IV

[a] Indicates the combined results of thousands of greenhouse tests.

[b] Temperature in degrees C/photoperiod in hours; light intensity in lux.

[c] Temperature 17°C±2°; light intensity 4000 up to 14,000 lux.

Besides the standard factors of the environment, other elementary factors are of influence, too. In the case of stripe rust Schröder and Hassebrauk (1964) found in Braunschweig that the spores germinated more slowly and less intensely if the sporulation happened in spells of cyclonic weather. They germinated relatively fast and more completely if they were produced during a change from cyclonic to anticyclonic weather. Sharp (1967) found in Montana and Alaska that the concentration of ions in the air influenced the germination of spores.

We know from our practical inoculations through the entire year that the culture of stripe rust in a climate greenhouse is not always guaranteed. Some days we inoculated wheat seedlings with poor rust material but obtained good success; other days (under the same conditions) we

inoculated with good rust material but obtained no success. We found this especially striking during November and December 1968 and January 1969 (Table 9).

The number of cultures of various origins used for inoculum on a given day are shown in Table 9. The appearance of the mature inoculum obtained from each culture for the next inoculation is shown to the right. If all samples reappeared in the same quality as in the original inoculum the number of cultures used would appear on the diagonal. In the case of the December 18 inoculation date, most of the material was shifted to the right upper corner, indicating a bad day for rust infection. In the case of December 25, the material was shifted to the lower left corner, indicating a good day for rust infection. Similar observations in the same time were made in Wageningen (Stubbs, *Personal communication*), which may be a sign for weather factors over Europe.

ADDITIONAL CHARACTERISTICS IN RACE DETERMINATION

In the search for additional characteristics in race determination, I attempted to utilize the variation in latent period[1] of the different rust cultures. Certain cultures are always quick to sporulate (short latent period) and some are slow to sporulate (long latent period). Cultures made up of individual races as defined by differentials and samples of given races obtained from different geographic areas were used as inoculum on Michigan Amber wheat. The inoculations were carried out in the greenhouse with the same cultures and wheat variety on different days. The results are shown in Table 10. Out of 95 inoculations on November 10, 10 were mature enough to be used for new inoculations after 14 days, 70 after 16 days, 15 only after 18 days, i.e., the first 10 were "quick", the last 15 were "slow" and so on, always in relation to the number of inoculations per day. The differences between 35 and 50 (November 12), 40 and 38 (November 17) and 42 and 52 (November 21) were not great enough to allow a "quick" or "slow" classification.

When these "periodicity" observations were summarized in relation to the number of transfers per culture (Table 11) they show additional race-differentiation to that we got out of the differential varieties tests.

With certain Japanese cultures we found an interesting relationship (Fuchs, 1965). All the cultures belong to race 42A as defined by virulence to Lee, but they reacted differently on the Reichersberg 42 (Lee supporting differential). The reaction on Reichersberg 42 was correlated to "quick" and "slow" latent periods. This observation may have been an expression of qualitative differences, and was confirmed with the second class differential Carsten V and some vigorous middle European races.

Other methods of race identification without differential varieties have been tried by Straib (1939) in using differences of spore germination and germ tube growth for stripe rust as well as for *Cronartium ribicola* J.C. Fisch. ex Rabenh. (Straib, 1953).

[1] *Time from urediospore inoculation to eruption of pustules for release of new spores (van der Plank, 1963).*

Table 9. Development of stripe rust in the greenhouse at different inoculation dates and with varying inoculum condition

Inoculation date	Condition of initial inoculum[a]	Number of cultures	Classification of inoculum[a] produced by each culture 14 to 18 days after inoculation				
			Good	Medium	Poor	Very poor	No infection
December 18, 1968	Good	25	10	4	2	2	7
	Medium	27	7	3	8	4	5
	Poor	30	1	1	2	9	17
	Very poor	29	0	1	2	2	24
December 25, 1968	Good	9	7	2	0	0	0
	Medium	13	10	0	2	0	1
	Poor	23	14	5	3	1	0
	Very poor	40	10	6	10	11	3

[a] Inoculum was grouped by estimating the sporulation and the quality of spores: Good = infection certain; Medium = very promising; Poor = infection doubtful; Very poor = infection very doubtful.

Table 10. Number of "slow", "quick", and unclassified infections of *P. striiformis* on a wheat variety (Michigan Amber) inoculated on different days

Latent period in days	Inoculation date and infection classification											
	Nov. 10	Class	Nov. 12	Class	Nov. 14	Class	Nov. 17	Class	Nov. 19	Class	Nov. 21	Class
14	10	Quick	35		8	Quick	15	Quick	9	Quick	2	Quick
16	70		50				40		86			
17					90						43	
18	15	Slow					38					
19			8	Slow	5	Slow			10	Slow	52	
21							2	Slow				
Total infections	95		93		103		95		105		97	

Table 11. Differentiation of races of stripe rust on the basis of latent period

Culture	Number of inocula-tions	Percentage of infection in each class		
		Quick	Unclassified	Slow
Race 7 from France	40	33	67	0
Race 8 from Germany	38	3	92	5
Race 32A from France	36	0	69	31
Race 32A from Switzerland	40	8	89	3
Race 3/55 from France	37	8	88	4
Race 3/55 from Netherlands	40	23	77	0
Race 3/55 from Switzerland	36	0	78	22

For stripe rust, Straib (1940) and later on Schröder and Hassebrauk (1964) stated that the differences between races were too small to serve effectively in determination.

The same seems to be true for differences in optimal germination temperatures and germination speed where a lot of statistical work is required, although these traits have some value (Manners, 1950; Fuchs, unpublished).

Attempts to show differences in physiologic races with electrophoretic patterns of spore proteins (Macko, Novacky, and Stahmann, 1967; Shipton and Fleischmann, 1969) are too recent to be discussed.

CLASSIFICATION, TAXONOMY

As long as there is no general applicability of new methods, we should apply classical race determination in cereal rusts, relying on differential varieties or "resistance genes" (monogene differentials).

Taxonomy and nomenclature are problems every determinator of rust races will meet. Kernkamp (1965, p. 822) stated, that either a world center for race determination and nomination for each cereal rust has to be established "with trained personnel, genetically pure differential varieties, and growth chambers so that all identifications could be made with the highest degree of precision," or that we carry on as is with each investigator naming a race "as best he can with the differentials and environment he has available." As shown in the survey of Johnson, Green, and Samborski (1967), some race determinators are already working with "genes"; however, many of them are not. For my own purpose and as a quintessence of the struggle with stripe rust "races" I am now going to use the abbreviations of the differentials themselves for race description in the sequence of their utility, which means: good differentials first (major genes?), less good differentials later (minor genes?),

additional differentials only in the case the corresponding main differential is susceptible. This approach is illustrated in Table 12.

New (good!) differentials can be added without difficulties with race numbers or additional figures. No longer useful differentials of former investigators can be missed without confusing the historical race key. I am rather convinced that only in the beginning it looks uncomfortable, and I hope that it provides more honest information. Isolating "V23.StD" from Spain and from Chile means that similar pathogenicities are valid in both places *as far as we know*. But indicating that race 3/55 was found in countries on different continents is dangerous because races which look identical on internationally used differential sets may very well be geneticially different (Guthrie, 1966; Hassebrauk, 1967).

Table 12. Proposed method of naming races of stripe rust based on differential variety abbreviation and specific reaction

Races (old)	Differential variety and abbreviation					
	Chinese 166 (Ch)	Heines Kolben (HK)	Vilmorin .23 (V23)	Lee (Lee)	Strubes Dickkopf (StD)	Spaldings prolific (Spa)
60A	Ch[a]	HK	[c]	Lee	StD	(Spa)[b]
60	Ch	HK			StD	(Spa)
27/53	Ch				StD	
54		HK			StD	
3/55			V23		StD	
32A			(V23)	Lee		Spa
20A		(HK)		Lee		

[a] Abbreviation written = the reaction of this differential is susceptibility and the race is virulent for this variety.

[b] Abbreviation in parentheses = the reaction of this differential is mesothetic and no clear cut resistance/susceptibility behavior is possible.

[c] Abbreviation absent - the reaction of this variety is resistance to the race.

CONCLUSION

To summarize, allow me to quote some scientists who are masters in their fields and who write much better English than I ever could.

There is the statement of Johnson, Green and Samborski (1967), "...ravages of the rusts are still not under control...." "It is a tribute to the enormous plasticity and adaptability of these pathogens, which have in one way or another circumvented the control measures that have been devised."

Also, Manners (1969) postulated the following: If and when a change to a new set of differential-hosts is made, the new set will need to satisfy the following criteria:

1) It will need to be efficient as defined by Person (1959), i.e., each host variety shall carry only one of the resistance genes.

2) It shall take into account mature plant as well as seedling reactions, so that the absurdity of having "field races" not integrated with the race determined by the more usual seedling tests made necessary by the present system in some cases, especially in yellow rust, may be avoided.

3) It should only include hosts that are genetically stable, and whose reactions are not influenced by environmental changes. As far as possible, hosts giving intermediate reactions should be avoided.

4) It is generally accepted by workers in the field concerned.

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FLOOR DISCUSSION

PERSON: Dr. Fuchs' talk made it clear that the identification of races and the whole business of dealing with their variability in cereal rusts is quite a big subject. It may be a blessing with the work that you are about to undertake with the white pine blister rust if you find it impossible to buy the idea of establishing physiological races. Are there any questions for Dr. Fuchs?

ZUFA: Should we try to continue to identify races of blister rust on the basis of ribes and what would be the importance of such work in our breeding of resistance to white pine bliter rust?

FUCHS: I think that's one of the questions I can't answer. I really don't know what you should do. Zadoks recommended something else, so perhaps you stay as happy as you are now. But of course, with the adaptability of the rusts, I think one day you will have to deal with races. They will come up; however, that's more judgment than knowledge.

ZADOKS. I will try to add a little bit. Your question was whether one should start identifying races using ribes. I think that identifying races using ribes would be completely feasible and that you would find them if you looked for them. On the other hand, I'm not sure that looking for races on ribes is really relevant to your problem. We have some information on this in annual crops. Let me cite a few. In oat crown rust, there are two types of physiological specialization. One on the pycnial host *Rhamnus*, and another one on the grain host. There are two froms of physiologic specialization which are somewhat linked but not completely. Another example is the *Poa-Ranunculus* complex which has been analyzed by Gauman in a completely different approach from ours. There are a great number of so-called micro-species of *Uromyces poae* Rabh. which cannot be distinguished on *Poa*, but which can be distinguished only because their pycnial stage appears on the different species of *Ranunculus*. Now, whether this is micro-species or physiological races is a matter of semantics, and what is important is that you get physiological specialization on the pycnial host. This is possible, with little physiologic specialization on a uredial host. So, there are a few examples in the literature which indicate that there are two different systems of physiologic specialization--one on the uredial host, and one on the pycnial host, which may or may not be related. Usually they are not.

PAWUK: I think a few years ago there was a publication out of Minnesota indicating physiological specialization on ribes from three or four isolates of *Cronartium ribicola* collected around the country. I don't remember the details on it, I just remember reading it. But, I think that they had tested a few species of ribes and found that there were some differences in symptoms.

LOEGERING: Why don't you call on Harry Powers to say something about that?

POWERS: I'm not sure about the races they reported on *C. ribicola*. Weren't there some questions raised about them?

DWINELL: From what I understand, that work has not been repeated and they are trying some new experimentation in an attempt to repeat it. They did not have, in fact, different varieties. They were not able to repeat the work so did not appear to have races.

LOEGERING: What I wanted Powers to tell about was the fact that he has races by differentiation. You tell them so I don't get it mixed up.

POWERS: This is my talk you're talking about. I prefer to wait until Friday to comment, but in short, yes, we have variation, which would roughly be an equivalent to your cereal rust basis, with *Cronartium quercuum*. One isolate was obtained from jack pine and the other from Virginia pine.

PHYSIOLOGY OF RUST RESISTANCE[1]

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ABSTRACT

An obligate parasite is one which can complete its life cycle in nature only on the living tissue of its hosts. Some strains of wheat and flax rusts have now been grown in axenic culture. The two critical issues are (1) what is the biochemical or biophysical basis of obligate parasitism? (2) what is the biochemical basis of genetically determined resistance or susceptibility? In the absence of host tissue the germination and development of rust uredospores normally stops with the formation of infection structures. Interaction with the host results in further development of the parasite.

In principle the following can be distinguished: Interactions between (1) parasite and environment, (2) host and environment, (3) "physical" interactions between parasite and host, (4) biochemical interactions between parasite and host mediated by (a) substances present before inoculation, (b) substances released after inoculation, (c) substances synthesized de novo after inoculation, e.g., proteins. The results of these interactions are often but not always seen in the effects of infection on the pattern of growth in the host. After infection respiration rate, the activity of the pentose phosphate pathway and the concentrations of many constituents, including RNA and auxir are increased. Water content is decreased. Such studies have usally been conducted at relatively late stages in disease development, but there is evidence that critical interactions between host and parasite occur very shortly after inoculation. Valuable insight has come from the use of (a) quantitative cytophotometric techniques for the measurement of DNA, RNA, total proteins, total histones, and lysine and arginine rich histones, (b) microradioautography of tissue sections after incubation with tritiated leucine, cytidine and uridine, (c) electron microscopy to examine the response of host nuclei to the presence of the parasite.

[1] *Editor's Note: Dr. Shaw's commitments have prevented him from rewriting his Study Institute paper before the publication deadline. With apologies he has provided a detailed abstract of his paper. The Editors have attached the Floor Discussion of Dr. Shaw's paper, since most of the discussion can be referred to the abstract.*

The cytophotometric results show that nuclear and nucleolar enlargement are accompanied by (a) parallel decreases in lysine and arginine rich histones, (b) increases in nuclear and nucleolar RNA, (c) increases in nuclear and nucleolar total protein, (d) no change in DNA until the nuclei finally collapse, when there is a dramatic loss of DNA. These may reflect a specific response to the parasite or a less specific response to stress.

The radioautographic experiments show that incorporation of tritiated compounds into host nuclei is doubled at the time that the cytophotometric measurements indicate a doubling or tripling of nuclear RNA levels. At this time electron microscopy indicates a marked increase in the density of the diffuse chromatin and a loosening of the dense chromatin of affected host nuclei. These changes may reflect an uncoiling of the chromatin and presumably also the increased protein content of the nuclei. They appear to be consistent with the supposition that host DNA is derepressed, perhaps through the loss of histones and that there is an accelerated synthesis of RNA and protein in the host. The possibility also exists that interaction triggers derepression in the parasite. Neither of these ideas is proven.

The effect of rust infection on the uptake of leucine-^{14}C and on its incorporation into protein was examined, using flax cotyledons. Uptake from the medium and incorporation into protein was increased 1.5 to 2-fold by rust infection. This effect was observed as early as 8 hours after inoculation in some experiments and was highly significant at 16 hours after inoculation. There was no significant difference between the responses of susceptible (Bison) and resistant varieties (Bombay).

Attempts to demonstrate the formation of new proteins (isozymes) within the first 24 to 48 hours after rust infection have failed. Nevertheless the possibility that this occurs and that such new isozymes mediate resistance by altering the balance between metabolic pathways or initiating new ones must remain as a working hypothesis.

The importance of fundamental biochemical and cell biological studies on host parasite relations cannot be underemphasized. The elucidation of the biochemical basis of resistance is not a short-term project and the selection and breeding of resistant varieties are likely to provide the most practical and economic approach to disease control for many years.

FLOOR DISCUSSION

PERSON: Thank you very much. We are on your side, really. We feel instinctively, that if the biochemists are successful they will, perhaps, discover some key metabolic reaction that may actually trigger the resistance response. If this could be done, it would certainly be a beautiful lead for genetical and other kinds of work. Is there anyone who wants to address any comment, criticism, or question to Michael Shaw?

VON BROEMBSEN: I noticed that in your work with Khapli and resistant varieties, you observed a decrease in proteins and RNA, two days after infection. This doesn't seem to go along with the idea of reduction of protein synthesis constituting a disease resistance mechanism.

SHAW: In Khapli, what we actually found was the same drop in histones, a less marked increase in RNA, and a less marked increase in fast green protein; but these increases were much more transient than in the susceptible variety. I passed over that very fast, I know. The most striking difference, really, between the Khapli situation and the Little Club one is that in Khapli you do get a decrease in DNA, which you will not see in Little Club until the infection is very old.

DAY: How many of the changes that you describe as occurring following infection are common to the kind of response which occurs when you injure the plant? In other words, how many of the changes are specifically induced by a pathogen?

SHAW: That is a very good question. I think that I am on record in print as saying that we don't know whether, in fact, we are dealing with some sort of specific response to the parasite or whether we are dealing with a less specific response to stress. I don't think you get nearly as extensive a response by injury as you do by infecting a susceptible plant with a parasite which will develop on it. The response of Khapli is much more condensed in time. Things happen quicker, and the whole thing falls off much more rapidly, but I don't think that we really have any critical evidence that these are specific responses. Somehow, we have got to try to determine whether they are specific or not.

FINCHAM: I was prompted by your remarks on host-parasite relations to think a little more about the gene-for-gene hypothesis we heard about this morning. As I understand this hypothesis, it means that for every gene in the host conferring resistance there is a gene in the parasite that would mutate in one step to overcome this resistance. Looking at it from a physiological point of view, do you see any reason why there should be only one gene in the parasite?

SHAW: No.

FINCHAM: And is this implied in the gene-for-gene hypothesis?

SHAW: I think we better let the gene-for-gene experts answer that. I, as a non-geneticist, don't see why there should only be one, but let me pass that to our moderator.

PERSON: I just have to agree with Dr. Shaw. I would think that having got a resistant host population, we would have a situation that would screen out the more successful members of the parasitic population, and that those that have a gene with a large effect that makes the parasite really successful in this situation will have an advantage over other smaller mutations. But, I don't see that the possibility is excluded of accumulating groups of genes in the parasite in response to a mutation in the host population that makes it resistant. So, I think that your question is well-based. There is no reason that I know of for concluding that you must have a gene-for-gene relationship in every case.

LOEGERING: Actually, there is one illustration of where this is true, and that is Watson's work on progressive mutation. Perhaps the reason this has never been seen in nature is because the final step in this progressive mutation is the only one that would be observed. This is a little bit of evidence, and as I said this morning I don't see why the strict gene-for-gene relationship has to be, only it has been. I would like to ask Dr. Shaw a question. What do you think of this idea which can be put in this way: Does the pathogen change the differentiation of the host cell back to meristematic development?

SHAW: We know that it does. Yarwood recorded years ago that there was a hypertrophy of bean leaf tissue at the infection sites of the bean rust. Recently, I'm not sure where it was, somebody recorded mitotic figures in the host that indicate there is induced division there. In the wheat system, of course, this doesn't occur. But we all know various rust systems where there is a great deal of cell division induced in the host.

LOEGERING: This is not the question I was asking.

SHAW: Oh, I'm sorry.

LOEGERING: It has been postulated that the physiological state of an infected cell with a haustorium in it is equivalent to a meristematic cell. Is there anybody who's compared these two types of tissue instead of comparing the susceptible with the resistant?

SHAW: No, I don't think anybody has done that. I was trying to say that there were certain similarities, and in some cases, you do get induction of meristematic activity as a result of infection. Certainly, you observe the induction of cell division, and this is one characteristic of the meristematic cell.

SCHÜTT: On one of your first slides, you showed data on water content, dry weight, etc. Does the data vary according to the resistance or susceptibility of wheat to rust? And, did you observe these same differences before inoculation?

SHAW: That figure simply referred to the changes in water status of the tissue under the influence of the parasite. Yes, the water content changes vary with the degree of susceptibility. No, I did not observe the same differences before inoculation.

ZUFA: In one instance you mentioned that the invaded cells of the resistant plant died.

SHAW: That happens eventually.

ZUFA: We call that hypersensitivity. In other cases, evidently the parasite lives together with the host in a kind of a symbiosis, sometimes for many years. Would any changes occur in the tissue of such a host tree and could it be considered resistant to the disease?

SHAW: I would guess that if you had a fungus living in contact with the host tissue, that host tissue would certainly not be the same as it is in the absence of the parasite, no matter how long the two stay together.

ZUFA: Evidently, it doesn't do any damage to the host.

SHAW: I don't think so. It's quite easy for me to conceive of the two organisms living side by side indefinitely.

VON BROEMBSEN: You emphasized that you thought there was a need for some good biochemical work on protein synthesis after inoculation. What, in your judgment, would be early, particularly in resistance reactions such as in Khapli where things happen fast?

SHAW: I don't think the Khapli system is a very good system to work with, but I am interested in what happens in the first 72 hours after inoculation. I am interested in everything that happens during that period. I picked 72 hours because of the results of one specific case that I am thinking about now, and this is with the SR-6 gene. You know there was some work done by Frank Forsythe of Winnipeg a number of years ago which I don't think has been cited enough or thougnt about enough. He went back to the idea of investigating the effect of light and temperature regimes on rust development, and the key point was that he found that whatever race of rust he was using on the variety that carried the SR-6 gene, which is temperature sensitive, he could reverse the situation from resistant to susceptible or susceptible to resistant by changing the temperature in the right direction up to approximately 72 hours after inoculation. Beyond that point, let's say it was somewhere between 72 and 90 hours, changing the temperature had no effect. So he had reached a point of no return and the thing was set. I think that this is a very important point which has not received enough attention. So early, in my terminology, means 24 to 48 hours.

VON BROEMBSEN: Did you show any data on protein synthesis for 48 hours?

SHAW: I think the earliest figures showed increased incorporation of leucine into protein as early as 8 hours after infection.

PERSON: Are there any other questions or comments?

MCDONALD: I would like to point out one very important aspect of the examples you gave which you didn't exactly state. You have a high degree of genetic control of both host and pathogen.

SHAW: Right--with the flax system.

MCDONALD: This is an extremely important point. Further, with respect to our natural system--or a system that hasn't been studied much, this is one of the things that really gives us fits in trying to do physiological work. We just don't have this control yet.

SHAW: Well, that's true.

CALLAHAM: For this very reason, do you consider that it is really worth while for us to go into sophisticated physiological studies of the response to infections or the nature of resistance in forest tree systems where essentially we are dealing with the wild host and microorganisms?

SHAW: That's a hard question to answer. I don't think it's going to give you any immediate practical solutions to your problems. As I said at the end of my talk, I think the genetic approach, if you want to call it that, is likely to be the more practical one. But, then you never know because maybe the *Cronartium*-pine system is one of these ideal systems that all the biochemical plant pathologists dream about where you could put your hand very easily on some specific chemical substance.

CALLAHM: I doubt it, but has anyone found one yet?

SHAW: No.

CALLAHAM: Thank you.

BASIC BIOLOGY OF RUSTS AND RUST DISEASE RESISTANCE: MODERATOR'S SUMMARY

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Each of today's speakers has covered a large area of basic biology. To attempt a summary of all that has been said would be a formidable task. Since I consider myself not qualified to make the attempt I have chosen, instead, to comment on a few points that were of special interest to me.

One point which has been emphasized several times today is that the problem of breeding for resistance to white pine blister rust is likely to be quite different from that of breeding for rust resistance in agricultural crops. A collection of these differences, taking wheat and stem rust as an example from agriculture, would certainly include the following:

White Pine	Wheat
Generation time: years	3 to 4 months is usual
Mating by cross-fertilization	by self-fertilization
Populations genetically diverse	homogeneous
Host genetically diploid	polyploid
Infecting rust haploid	diploid (dikaryotic)
Alternate host present	generally absent

There are probably other ways in which the two situations differ sharply. It seems worthwhile, therefore, to re-emphasize the point made by previous speakers, that breeding procedures which are known to be successful in agriculture need not be successful in forestry.

Because large acreages are often sown to a relatively small number of "pure" cultivars it is not usual in agriculture to approach disease problems from the point of view of populational or ecological genetics. One result of this is that we actually know very little about the genetics of non-agricultural, or naturally occurring, parasitic systems. Since the kind of disease epidemic that is familiar to agriculture is not characteristic of undisturbed, natural populations it seems evident (to me at least) that regulating mechanisms are present in natural systems which operate in such a way as to keep host and parasitic populations in balance with each other.[1] Knowledge of such regulatory mechanisms (if they exist) would provide the basis for new approaches to the solution of disease problems in agriculture as well as in forestry. Since I believe that such mechanisms do exist, I view the white pine blister rust problem as an opportunity to discover new principles in the biology of disease.

[1] *See paper by Hoff and McDonald, these proceedings.*

An important question at this juncture is to ask if anything has been learned of disease resistance in agricultural crops that may be carried over to the study of natural populations. We have heard papers today on gene-for-gene relationships, and on horizontal and vertical resistance. It is evident that the use of major genes can give dramatic results. Because introduction of a major resistance gene can evoke equally dramatic single-gene responses from the parasitic population (this is probably how gene-for-gene relationships originate), there are many plant breeders who now favor the use of horizontal (i.e., multigenic) resistance. But we heard today also that Dr. Zadoks views the two types of resistance, horizontal and vertical, as representing the outer limits of a resistance continuum that ranges between the two extreme types. Van der Plank also mentions in his book that the terms "horizontal" and "vertical" do not readily accommodate resistance that is intermediate (i.e., digenic or trigenic). The preference of some breeders for multigenic resistance, and the hope that this kind of resistance may confer longer-term benefits to agriculture, may very well have originated from an oversimplified view of the problem.

We can also ask whether major and minor genes both have a role to play in naturally occurring populations. When we recall that the *demissum* genes for potato resistance to late blight were in fact collected from naturally occurring wild-potato populations of South America, the answer to this question seems to be "yes". As well, certain major genes for resistance to crown rust have been transferred to cultivated oats, through breeding, from wild populations of *Avena sterilis* L. Several other examples of major-gene resistance obtained from species in nature are listed by Watkin Williams (1963).

Evidence for the existence of horizontal resistance in nature is harder to find. This is not surprising, since the genetic basis for this kind of resistance is inherently difficult to demonstrate. The "field-resistance" of potatoes to late blight seems to have arisen "naturally" (i.e., not through artificial breeding) during the decades immediately following the great potato famine in Europe. There is no good reason, it seems to me, for thinking that this kind of resistance does not also exist, as an integral component, in naturally occurring systems of parasitism.

Accepting the premise that major and minor genes are both present in naturally occurring systems of parasitism, we can next ask the question: how do they work together in such a way as to regulate the disease? Although there is no good answer to this question as yet, some hints as to possible answers are mentioned below.

According to Pimental (1961) the specific interactions between "feeding" and "eaten" populations (whether these interactions involve predator-prey, herbivore-plant, or host-parasite relationships) are kept under control in nature through operation of specific regulating mechanisms. The rule, in all these relationships, is that the feeding species must feed without endangering survival of the eaten species. (In financial terms this would be a question of living on the interest without withdrawing the capital). Some of the evidence for regulating mechanisms is of a negative kind: when a species is introduced as an immigrant to a new community, it commonly increases to outbreak levels in a very short time; we infer that it does so because it is newly freed from its normal regulatory restraints. Pimentel has identified at least one such regulatory mechanism, "genetic feedback", by which interacting species

are brought into closer genetic balance. The operation of genetic feedback was first demonstrated through computer studies on imaginary populations. These studies showed that, under appropriate conditions, a system in which the relative numbers of those eating and those being eaten out of balance will generate a series of regular fluctuations, the amplitude of which will decrease as stability is approached. The decrease in amplitude is mediated through genetic feedback. Pimentel has succeeded in demonstrating the operation of genetic feedback in at least one parasitic system (the house fly and a parasitic wasp which feeds on house-fly pupae) in the laboratory. He also points to the evidence gained through use of the myxomatosis virus to control the european rabbit in Australia. Anyone who is familiar with the history of wheat stem-rust in North America will also be familiar with the operation of genetic feedback.

A second hint as to how natural systems may be self-regulating originated with the suggestion by E. B. Ford (1965) that resistance to disease may be one of the factors that can lead to continued maintenance of two or more alleles within a single population, and hence to stable genetic polymorphism. This possibility was examined (for the rusts) by C. J. Mode (1958), and, more recently, by myself (Person, 1966). An essential feature of the models we have proposed is that regulation is achieved through more or less regular cyclic fluctuations in the frequencies of "major" resistance alleles. What is envisaged is a series of genetic changes, mediated by genetic feed-back, which repeat as time progresses so that the parasite is presented with a host population whose genetic composition is constantly changing. Keeping in mind that it is through continuous replacement of host varieties that stem rust of wheat has been held in check, these models seem not to be entirely without merit. (As well, the introduction and use, by Borlaug, of multiline varieties has been successful; in this approach the parasite is presented with spatial, rather than temporal, discontinuities of host genotype. It is possible that both kinds of discontinuity co-exist in naturally occurring populations.)

Hints of this kind can be taken as only crudely suggestive of the mechanisms for self-regulation that may actually exist in nature. For this reason it will probably not be possible to select, in advance, any "best" approach to the solution of the white pine blister rust problem. It is my opinion that the populational-ecological approach must be given prominance and, in such a case, that a great deal of research will be needed. It is in this undertaking that I see the opportunity, mentioned earlier, of discovering important new principles in the biology of disease.

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PANEL II

ASSAY OF THE WORLD'S WHITE PINE BREEDING MATERIALS
Richard T. Bingham MODERATOR

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INTRINSIC QUALITIES AND GROWTH-POTENTIAL OF *PINUS CEMBRA* AND *PINUS PEUCE* IN EUROPE

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ABSTRACT

Some details concerning growth and qualities of native European white pines are reported. There are only the two native species--*Pinus cembra* in the Alps and the Carpathian mountains and *P. peuce* in the mountains of the Balkan peninsula. *P. sibirica* (i.e., *P. cembra* var. *sibirica* grows in northern Siberia and covers a great part of this country. All of these species are from high altitudes or latitudes, and so we find they exhibit very slow juvenile growth. Growth rate of *P. peuce* may increase with time, but *P. sibirica* is mostly slow growing throughout its rotation and *P. cembra* from the Alps in Europe and probably the mountainous forms of *P. sibirica* are even slower growing.

The trees of these species reach great age, especially *P. cembra* (and *P. sibirica*) where an age of 300 years and more is common. Height growth and wood production is satisfactory if site conditions of the stands are considered. In their natural mixed stands individuals of these species exhibit the best growth.

Wood quality is good and the wood is in high demand, so the price is fairly high.

Both species are used for mountainous forestry and are very important for reforestation of the subalpine zone; in this zone they are also important on watersheds, stabilizing avalanche areas and reducing effects of flash floods.

Introduced white pines (*Pinus strobus* and *Pinus wallichiana* excepted) are not planted in forest stands in Europe, and are not reported upon here.

INTRODUCTION

In Europe the pine flora is quite impoverished, and in common with this only two species of white pines are native. These two species are *Pinus cembra* L., the Swiss stone pine (Zirbe, Arve, etc.), with its distribution in central Europe in the highest forest zone of the Alps and the Carpathian Mountains, and *Pinus peuce* Griseb., the Balkan pine

(Bjala Mura, Molika, Rumelische Strobe) with its distribution in the highest parts of the mountains of the Balkan Peninsula in the southeastern part of Europe. In addition, there is a species (or subspecies)--*Pinus sibirica* Du Tour (Kedra, Siberian stone pine; i.e., *Pinus cembra* var. *sibirica* Loud.)--with a wide distribution in the forests of northern Asia and in small areas of the Asiatic Mountains (Ural, Transbaikal and Altai). *P. sibirica* is the most important of all these white pines with a botanical range of about 28.8 million hectares over most of western and central Siberia. It comprises 7% of all timber there, but 85% of these white pines are older than 200 years (Kügler 1962, 1969). The area of *P. cembra* is quite limited, because of its distribution only near alpine timberline. It extends to about 30,000 ha (reduced area, mostly in the Austrian Alps). The same distributional pattern holds for *P. peuce*; it grows on sites only near timberline. Its reduced area is only about 12,000 ha., most of it in southern Bulgaria (Nedjalkov, 1963). *P. cembra* stands add up to 3% of the timber of the countries Austria, northern Italy, and Switzerland; *P. peuce* stands to 3% in Bulgaria, but less in Yugoslavia and Albania.

Introduced white pines in Europe [mostly *P. strobus* L. with some *P. wallichiana* Jacks. (syn. *P. griffithii* McClell.)] occupy only a small area (see R. Schmitt, these proceedings). Other introduced white pines are found mostly in gardens, as single trees under varying growth conditions. A small stand of *P. monticola* Dougl. was reported in the British Isles by MacDonald *et al.* (1957). At certain places in central Europe we can find small, introduced stands of *P. peuce*, and in the Scandinavian north and in the north of European Russia (Archangelsk Region) we find some introduced stands of *P. sibirica*, especially planted because of their edible seeds.

THE NATURAL DISTRIBUTION OF *PINUS CEMBRA*, *P. PEUCE*, AND *P. SIBIRICA*

PINUS CEMBRA

As shown in the map (Figure 1) the distribution of *P. cembra* is restricted to the Alps and to small parts of the Carpathian Mountains. This species is a tree of the forests near timberline. It climbs high up in the zone of single trees above this line, as a pioneer for the subalpine zone (Holzer, 1963). In its natural distribution it may occur in at least two different forms--as a forest type and as an open woodland mostly of stunted trees providing a ground cover in the high elevation "Kampfzone". A good botanical characterization of this species is given by Kirchner, Loew, and Schroeter (1908). Apparently we should differentiate these two ecoptyes, as indicated by differential growth of progenies and graftings (Holzer, 1969). The low-elevation native *P. cembra* stands extend from 1100 m to 1500 m, as individual trees and forests respectively. The principal zone extends from 1700 m to 2000 m, 2100 m sometimes in the Central Alps; above this zone we find single trees up to the tree border with highest individuals up to 2700 m (Moser, 1960; Marchetti, 1961; Nevolè, 1914; Rikli, 1909; Rubner and Reinhold, 1960). The highest stands are found in the western Central Alps; tree line descends towards the east (Fuschlberger, 1928). The area in the Carpathian Mountains is much smaller, likely because of the lower elevation of these mountains, but shows similar conditions; the extension begins at 900 m and goes up to 1986 m for the highest known tree (Fekete and Blattny, 1913). Greatest value of *P. cembra* is probably for watershed and avalanche protection.

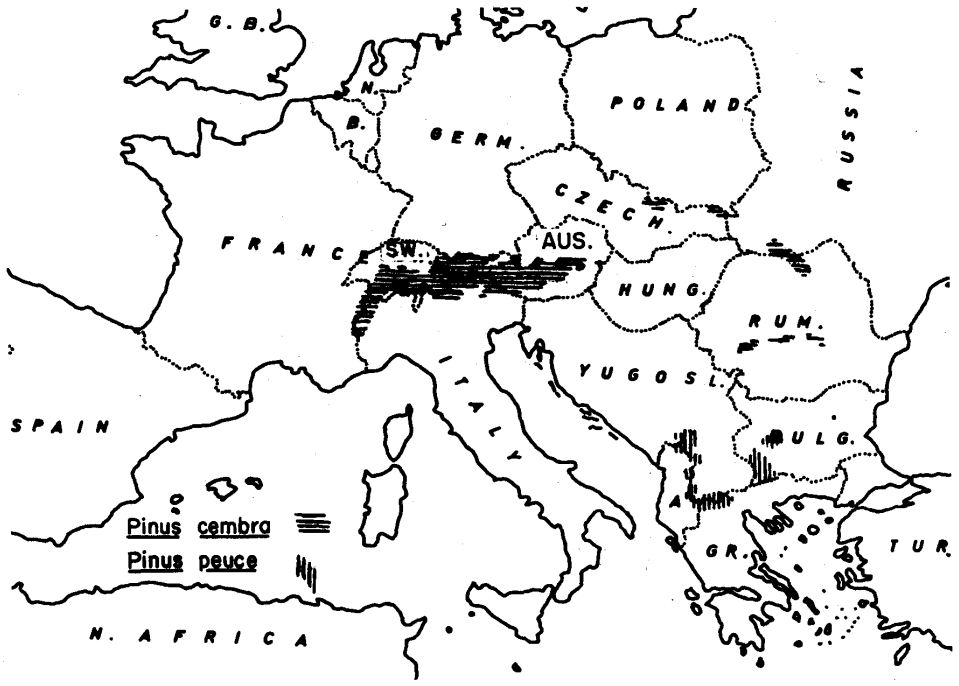


Figure 1. Map of central and southern Europe with the natural distribution of *Pinus cembra* and *P. peuce*, after Rubner and Reinhold (1960), Mirov (1967), Nevolè (1914), Fekete and Blattny (1913), and Adamovic (1909).

The stands in the Alps very often were reduced during the last centuries by lumbering and other uses made of this tree. Thus there are many places where *P. cembra* is now missing, or at which the timberline is lowered because this species is not present. (*Picea abies* (L.) Karst. is not able to grow higher up). We find no association of *P. cembra* with soil or rock type, but growth of this species is poorer in calcareous mountains and so it is easier to displace. Other species in these stands are *Larix decidua* Mill., up to the timberline, and especially *Picea abies* in the more continuous forests.

PINUS PEUCE

Similar conditions are found for *P. peuce* in the mountains of the Balkan Peninsula (Fig. 1) (Adamovic, 1909; Müller, 1928; Nedjalkov, 1963; Hengst, 1967); like *P. cembra* this species is distributed near the upper timberline and extends to about the same altitude. Beginning with single trees in the forests at 1200 m we find the maximal distribution (60 to 70% of all trees) in the zone of 1700 m to 2200 m, very often in pure stands. Above this area we also find single trees in the "Kampfzone" between timberline and treeline, similar to *P. cembra*. The highest trees are at 2600 m in Montenegro (Müller, 1928; Schenck, 1939). The forests of *P. peuce* also are mixed with *Picea abies*; but *P. peuce* is restricted to the soils of basic reaction (it is replaced by *Pinus heldreichii* Christ. on the calcareous soils (Hengst, 1967)). Greatest value of *P. peuce* is probably for watershed and avalanche protection.

PINUS SIBIRICA

P. sibirica has its natural distribution in the north of Siberia and extends to the (northern) timber line, too. These forests are called Black Taiga and contain the species *Abies sibirica* Ledeb. and *Larix gmelinii* Rupr. Litvin (sometimes *Picea obovata* Ledeb.) in mixture (Belov, 1963). *P. sibirica* comprises 5.3% of these stands (Buchholz, 1959). We also find altitudinal distribution in the mountain regions, and in latitude it is very widespread. Mirov (1967) reports three varieties of this tree: the common form in the northern Siberian plains, a variety called *P. coronans* Litv. (a mountain form in the Altai), and "forma *depressa*" Komarov in the Transbaikal (which also seems to be a mountain form). The area of the Siberian stone pine exceeds nearly 28.8 million ha, and so it is much more important than the two native European white pines. Production of nuts (the seed) for men and animals is very important, and sables bred for fur and meat are fed with the nuts (Kugler, 1962).

SILVICULTURAL REQUIREMENTS OF *P. CEMBRA* AND *P. PEUCE*

For best growth both *P. cembra* and *P. peuce* prefer light and humus soils; heavy grassy soils very often make growth impossible. *P. cembra* grows best in the subalpine shrub vegetation (Forstl. Bundesversuchsanstalt, 1961, 1963, 1965, 1967; Holzer, 1961). *P. peuce* does not like calcareous soils. Neither can withstand shade except in their youth (very often seedlings are growing below *Rhodendron* and *Vaccinium* shrubs; later in life the plants have a strong need of light. The roots lie parallel with the ground surface. A humid climate with wet air in summer is preferred, and these species can withstand much snow in winter. They are not injured by low-temperature extremes (Holzer, 1959), and it is thus that we find the most extensive and best stands on the north- and northwest-facing slopes (Forstl. Bundesversuchsanstalt, 1961, 1963, 1965, 1967; Nevolé, 1914; Müller, 1928; Tranquillini, 1956, 1958).

GROWTH POTENTIAL AND INTRINSIC QUALITIES, *PINUS CEMBRA*, *P. PEUCE* AND *P. SIBIRICA*

The growth characteristics of both *P. cembra* and *P. peuce* are similar and so we can speak about them without distinction. Usually we find very slow juvenile growth, late cumulation of growth, and then long-continued growth so that there remain some very old trees in the stands.

JUVENILE GROWTH

Juvenile growth is very slow with these species, even in the better stands at optimal elevations. Slow growth persists for 20 to 30 years; more than 5 years pass before an erect terminal shoot is attained as shown in Figure 2(Figala, 1927; Oswald, 1963; Holzer, 1963, 1969; Müller, 1928). Growth of only a few cm per year is general, and we get the same results when seedlings grow in natural high mountain zone (Oswald, 1963) or in a warmer climate (Holzer, 1969). *P. sibirica*, however, grows somewhat faster and the youthful period of restricted growth is shorter. Consequently, *P. sibirica* plants of nearly double the growth attained by the alpine *P. cembra* are produced at an age of 10 years (Holzer, 1969).

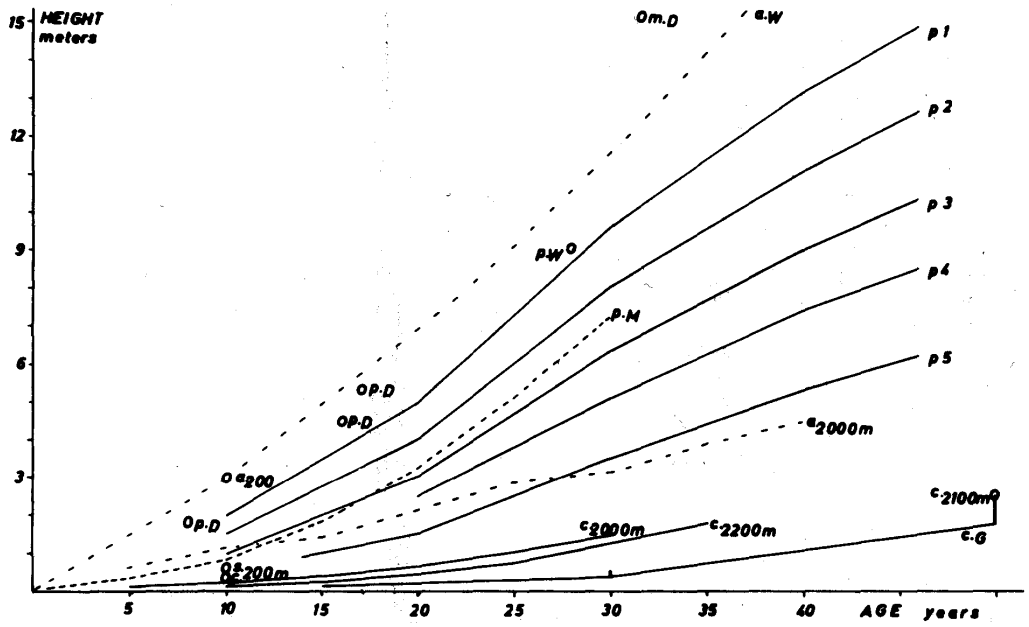


Figure 2. Juvenile growth of European white pines:
$p1...p5$ = *Pinus peuce* after growth curves (Nedjalkov, 1963, Bulgaria);
p_D = single-tree data (after MacDonald *et al.*, 1957, England);
p_M = after Müller (1928, Bulgaria, natural);
p_W = after Mayer (1965, Austria, planted);
c = *Pinus cembra*, with elevation of growing place (200 m, Holzer,1969; 2000 m and 2200 m, Oswald, 1963);
c_G = after Gregori (1887, natural);
s = *Pinus sibirica* (grown in the nursery of Vienna, 200 m, Holzer,1969);
a = *Picea abies* for comparison at 200 m (unpublished data, Forstliche Bundesversuchsanstalt, Vienna),2000 m (Oswald, 1963);
a_W = data after growth curves (Frauendorfer, 1954);
m_D = single value for *Pinus monticola* in England (MacDonald *et al.*, 1957).

At about this age (10 to 15 years), *P. cembra* and *P. peuce* plants begin to make regular growth every year, with terminal shoots reaching a length of 10 to 20 cm (Oswald, 1963; Gregori, 1887; Müller, 1928; Nedjalkov, 1963). Growth differences that appear at this age may be associated with inherent parental growth capacity, with altitudinal provenance, or with site. Presently we don't know much about this; but we may theorize that differences are partly inherent because the growth of graftings from adult plants is similar to the growth of seedlings from the same parents (Holzer, 1969).

In the natural range seeds are distributed by jays and squirrels (Oswald, 1956). As the stand ages very often we may find individuals of

P. cembra that are 50 years old, but only a few cm in height (Figala, 1927; Oswald, 1963), especially in stands above timberline. Here climate is very severe; but *P. cembra* is very resistant to such high-elevation climatic conditions (Holzer, 1959; Tranquillini, 1956, 1958). Under these severe timberline conditions medium height at age 50 is about 1.5 to 2.5 m for *P. cembra* in closed stands (Gregori, 1887). It is much greater (about 6 to 15 m) for *P. peuce*, because the yearly growth of this species is about 30 to 50 cm (Fig. 2, Müller, 1928; Nedjalkov, 1963). This best height growth of *P. peuce* is found at an age of 20 to 40 years (Müller, 1928; Nedjalkov, 1963). So we find much better growth in *P. peuce* than in *P. cembra*, because the best shoot growth of *P. cembra* is about 20 to 25 cm. Even though *P. peuce* is supposed to be a fast growing white pine, the very slow early growth of this species gives difficulties - especially at nursery stage.

Both species are resistant to frost throughout the year, especially to late frost (Müller, 1928); only winter coldness and temperatures fluctuating around the freezing point of the needles may injure the leaves (Holzer, 1958, 1959; Tranquillini, 1964; Tranquillini and Holzer, 1958).

ADULT GROWTH POTENTIAL

As shown in Figure 3 the height growth potential of European white pines is not very high, when compared with other native species like Norway spruce or Scots pine. The height growth begins very late but lasts for a very long time. Both species are adapted to cold mountainous climates with long winters and short summers. The slow growth appears to be under genetic control - it cannot be accelerated by planting into warmer climates. The longer vegetation period (growing season) at lower sites does not accelerate growth through secondary, or lammas-shoot growth (Holzer, in press). Adaptability to zones colder than the source locality is possible only with restriction of growth potential; in fact *P. cembra* is able to grow at an average temperature of 0°C per year (Fuschlberger, 1928; Tranquillini, 1957, 1964).

The best height growth is found in *P. sibirica*. Here we have seven classes of height growth potential (Fig. 3, after Leskov and Semeckin, 1963); the best individuals attain heights up to 40 m after 300 years, but at an age of 100 years the best heights are only 25 m. *P. peuce* in the Balkan Mountains reaches a height of 26 m at an age of 160 years (Nedjalkov, 1963). Most comparisons with *Picea abies* or *Pinus sylvestris* L. in natural stands show that these latter species are growing faster, but not in the best region of the white pines (Hengst, 1967; Nedjalkov and Krastanov, 1962; Schikov, 1965). The height growth of *P. peuce* on the best sites is about the same as that attained by *P. sibirica* on site class III (Fig. 3). The alpine *P. cembra* shows the poorest height growth of all (Figala, 1927); on its best sites (Class I-III) it only reaches heights equivalent to those of *P. sibirica* on its 3 poorest sites (Classes IV-Va). The best, selected trees of *P. cembra* in Austria, however, are on the average, one site class better (Holzer, 1969). They reach about 26 m at an age of 150 years. Here also the comparison with alpine *Picea abies* (Fig. 3) shows that the growth of *P. cembra* is not good at optimal climatic conditions.

It is the same way with diameter growth and wood production; we can see the slow growth of all these white pine species. However, diameter growth is much better than height growth in all three species. Most

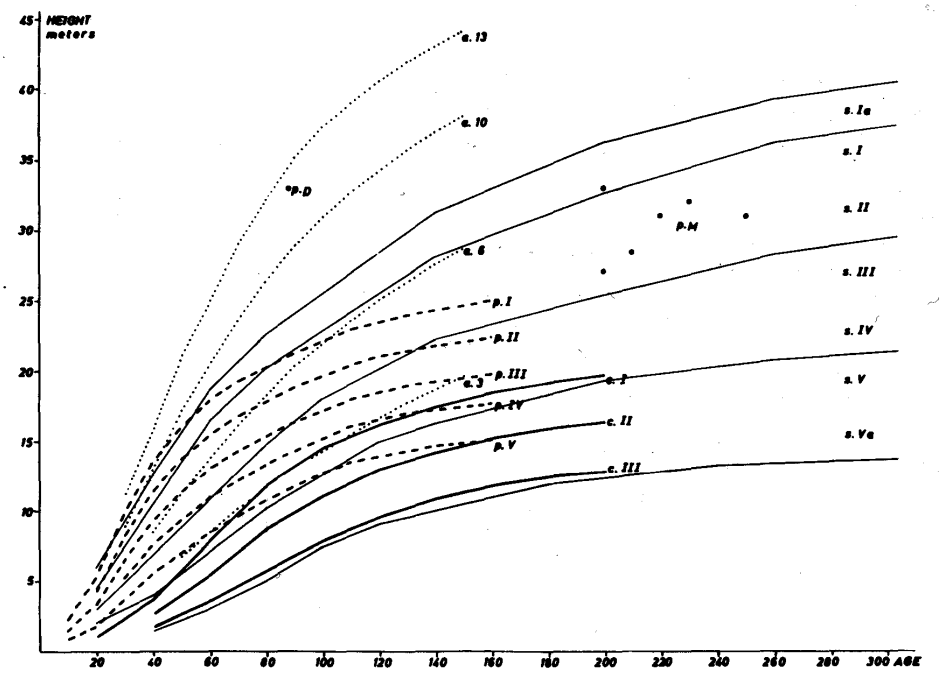


Figure 3. Adult height growth of European white pines in comparison with alpine *Picea abies:*
*a*3...*a*13 = *Picea abies* (after Frauendorfer, 1954);
*c*I...*c*III = *Pinus cembra* (after Figala, 1927);
*p*I...*p*V = *Pinus peuce* (after Nedjalkov, 1963);
*s*Ia...*s*Va = *Pinus sibirica* (after Leskov and Semeckin, 1963);
p_D = single data for *Pinus peuce* in Great Britain (after MacDonald *et al.*, 1957);
p_M = single-tree data for *Pinus peuce* in natural stands (after Müller, 1928).

important is the long lasting, uniform growth of all three species; it results in good volume production in old and very old trees. The best trees at an age of 300 years may have a diameter of 100 cm and more (Jamnicky, 1964). A diameter of 60 cm at breast height is common in 200 to 250 years old *P. sibirica* (Hempel and Jung, 1968). Two-hundred-year-old *P. cembra* trees may reach 40 cm and more (Figala, 1927; Gregori, 1887), and selected trees of Swiss stone pine in Austria reach the same dimensions as *P. sibirica* trees (Holzer, 1969). Similar dimensions may be found in *P. peuce* too (Nedjalkov, 1963).

The crown form of these species in general is narrow with small branches except that in open stands--above timberline especially--very often we find individuals with heavy branches, multi-forked trunks, and sometimes with candelabrum branches or a spherical crown. Stems without defects are rare.

WOOD-VOLUME PRODUCTION

Because of the good and long-lasting diameter growth, wood volume production of these white pines is satisfactory in most cases, especially where considering that the environmental conditions in their natural areas tend to restrict growth. The basal stem gives especially good yields when it reaches its best age. There are as yet no yield tables for Swiss stone pine, but the comparison with the values for *P. sibirica* or *P. peuce*, classes IV and V (Hempel and Jung,1968; Nedjalkov, 1963, respectively), gives usable values for yield. Production is especially high in single trees with full crowns, as common in the alpine distribution. The comparison with the yield tables of alpine *Picea abies* (Frauendorfer, 1954, after Guttenberg) shows that higher in the mountains *P. cembra* gives better yields than *Picea abies*. We find a distinct change for the better as we ascend in elevation: at the lowest distribution of *P. cembra* where it grows slowly, *Picea abies* gives much better production; at the transition area the production is about the same for both species; and in the principal zone of *P. cembra* its production is better than that of *Picea abies*. The trees at timberline and above--especially single trees--are growing slower and give less production; in many cases stems are forked in both species, so that there is still no wood harvest in this zone. However, man is glad to have any tree growth at all in this area.

WOOD QUALITY AND USES

The wood of both *P. cembra* and *P. peuce* has the same qualities that wood of white pines share in common. It is light in weight (sp.gr. about 0.41-0.43, when dry) and does not shrink much (2.4% from fresh to dry wood, Figala, 1927; Nedjalkov, 1963). The wood is easily worked and so it is used for carving, and often for barrels and buckets. Because of its nice structure it is also used for furniture and for sashes and doors or interior trim in lodgings. Many other uses of former times are not common now, because the worth of this wood is too great. The value of a *Pinus cembra* stem, for example, is about 3 to 6 times higher than the value of the same size saw-timber of *Picea abies* or *Pinus sylvestris*, and for sawmill usage exceeds about \$40-\$70 per m^3 (i.e., 424 bd ft). This value is possible only because of specialty demand, but it takes the tree a good many years to reach suitable dimensions.

IMPORTANCE OF EUROPEAN WHITE PINES FOR MOUNTAINOUS FORESTRY

The great importance of native European white pines is a result of their adaptability to subalpine climate and their use as protection woods. In Austria a group of scientists is working on ecological and physiological problems of *P. cembra* (many papers by these workers are given in publications of the Forstliche Bundesversuchsanstalt, 1961, 1963, 1965, 1967). These papers show the great importance--but also the great difficulties--of managing *P. cembra* in the alpine valleys. Many thousands of ha could be reforested with this species to protect lands and people against avalanches and flash floods. It should be possible to restore *P. cembra* to the forest area it occupied 200 and more years ago (at least 100,000 ha); many trees since have been cut down to increase pastureland. This species is nearly the only one that is able to grow high up in the subalpine zone of the Alps and the Carpathian Mountains, sometimes 200 and more meters above present timberline (Forstliche Bundesversuchsanstalt, 1967;

Jamnicky, 1963). Only *Larix decidua* reaches a similar altitude, but doesn't form closed stands as is partially done by *P. cembra* (Tranquillini, 1956, 1964; Stern, 1966; Holtmeier, 1969; Piskun, 1964).

Similarly *P. peuce* forms the upper tree line of the mountains of the Balkan peninsula and protects man and the land (Adamovic, 1909).

RESULTS OF ARTIFICIAL PLANTINGS OF WHITE PINES IN EUROPE

As indicated in the introduction only limited plantations of white pines exist in Europe, most of them being of *P. peuce* and *P. cembra*. *P. peuce* has the reputation of being a good tree for plantations in central Europe. At many places small stands were planted. But few foresters are satisfied, especially by the slow juvenile growth (Thümmler, 1962). Schenck (1939) reports that the yield of *P. peuce* amounts to only about 2/5 that of the blister rust-devastated *P. strobus*. Plantations of *P. peuce* on slopes in West Germany reach the height of 20-year-old *P. strobus* not earlier than at 50 years age. At the forest garden of Vienna *P. peuce* was planted in a mixture with *P. strobus*. At 32 years age the *P. strobus* had all died, probably from blister rust, but the *P. peuce* was growing quite well (Mayer, 1965, Fig. 1). The growth form is pleasing and it is resistant enough against winter injury so that this tree is recommended for smaller gardens (Schenck, 1939).

P. cembra is planted at several places in Europe; most of them are with *P. sibirica* in northern Europe (Scandinavia and Russia; Stefansson, 1955; Ivanova, 1963; Orlov and Tarabrin, 1959). Many plantations were established at times of famine, about 200 years ago, because the seeds were needed for food. Later, many plantations of *P. sibirica* were established because with age they outgrew *P. cembra* (Tomarewskij, 1957). King Charles the Great, who lived in the ninth century, set this tree aside as a fruit tree and nobody was allowed to fell it. In England *Pinus cembra* is planted at many places, but it is not recommended for forestry (Dallimore and Jackson, 1954). Another plantation, now 50 years old, was made in Yugoslavia (Silic, 1960). But growth is slow everywhere and so far no useful forest stands exist from plantations. *P. cembra* and *Pinus aristata* Engelm. have been planted in Iceland since 1899, with good success (Bjarnason, 1965).

Small stands of *P. monticola* Dougl. are reported by MacDonald *et al.* (1957) in Great Britain, and by Schenck (1951/52) from 4 places in Germany. The first authors reported two fast-growing trees, that grew 60 feet high within 21 years; another stand reached 50 feet in height and 27.5 inches girth within 32 years (see Fig. 1). Schenck (1951/52) reported 4 groups of *P. monticola* in Germany; their height was 6 to 9 m at an age of 20 to 23 years and their diameter varied between 7 and 27 cm. Susceptibility to blister rust was reported as variable.

Schenck (1939) made a report about all foreign trees in Germany. In it no other white pine is reported to be planted there except in botanical gardens. Most introduced white pines are resistant enough against winter injury, but the blister rust resistant species represented (*Pinus aristata* Engelm., *Pinus balfouriana* Grev. and Balf., *Pinus koraiensis* Sieb. & Zucc., and *Pinus parviflora* Sieb. & Zucc.) all come from mountainous, high-elevation areas and are no faster growing than the native European white pines (Schenck, 1939).

In the Mediterranean, subtropical countries there is a possibility to introduce several Central American and southern North American white pines, but these are not hardy enough for temperate zone (Morandini, 1961).

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FLOOR DISCUSSION

Moderator Bingham withheld discussion on this paper until after Dr. Hans Hattemer (substituting due to illness of Dr. Richard Schmitt) had read Dr. Schmitt's closely related paper. Discussion of both papers follows Dr. Schmitt's paper.

INTRINSIC QUALITIES, ACCLIMATISATION, AND GROWTH POTENTIAL OF WHITE PINES INTRODUCED INTO EUROPE, WITH EMPHASIS ON *PINUS STROBUS*

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ABSTRACT

Since the European forests are composed of relatively few tree species, early attempts were made to enrich them with fast growing exotics. One of the first to be introduced was the eastern white pine (*Pinus strobus*). This species showed good qualities and proved to be well adapted to the climate of the deciduous forests of western Europe, especially in the warmer parts with a more continental climate.

In eastern Europe forests the eastern white pine is completely hardy, withstands late frosts; grows on difficult soils, and reproduces itself naturally with ease. It is a semi-tolerant tree and thus is especially adapted for use in mixtures with hardwoods. Its dead needles enrich devastated soils and keep weeds down. Stem forms are good and growth is excellent--no European forest tree will give a higher yield on any site.

It is heavily damaged by game animals, by the honey fungus (*Armillaria mellea*), and by the blister rust fungus (*Cronartium ribicola*).

Extent of European *P. strobus* plantings may be estimated to 6,400 ha, most of it in West Germany with a center in Hesse, middle Germany, and in Austria. Moreover, it is found in mixed forests on more than 20,000 ha. In the last decades the establishment of new stands of this valuable species was curtailed because of the danger of blister rust.

The introduction of certain provenances of the eastern white pine to the higher mountains (i.e., higher than 600 m above sea level) was a failure; the trees grew poorly and were heavily damaged by ice.

Other introduced white pines occupy only a negligible area. *Pinus griffithii* (syn. *P. wallichiana*) is not hardy enough for northern and central Europe, but perhaps will grow in the warmer southern parts. *Pinus monticola* proved to be as slow growing as *P. peuce* under average European conditions.

INTRODUCTION

European forests are composed of relatively few tree species, compared with those of similar temperate regions in America or Asia. This poverty of our flora, mainly due to the east-west direction of the Alps which prevented most tree species from retreating to warmer regions during the glacial period, is more pronounced in the fast growing conifers than in broad-leaved trees. Therefore, because the deciduous forest of western Europe was an economic mainstay in preindustrial times, the European foresters soon tried to enrich it with foreign species. One of the first introductions, perhaps the very first, was eastern white pine (*Pinus strobus* L.).

HISTORY OF EUROPEAN INTRODUCTION AND ADAPTATION OF EASTERN WHITE PINE

P. strobus was first recorded to be growing in the Royal Gardens of Fontainebleau, France, in 1553 (Lanier, 1961) and at Badminton, Great Britain, in 1705 (MacDonald *et al.*, 1957). Like most exotics it was at first planted out of curiosity as a specimen tree in arboreta and parks. Since it also showed good growth elsewhere in Europe, soon small plots and plantations were established at intervals through the late 18th and 19th centuries. This was especially true in Germany during the great reforestation period about 150 years ago. For example, in 1790 near Wolfenbüttel (Borchers, 1951/52), and 1795 in the community forest of Frankfurt/Main, mixed stands of Scotch pine (*Pinus silvestris* L.) and eastern white pine were established by seeding; now the fourth generation of these white pines is growing just south of Frankfurt (Eckstein, in press).

In France stands of *P. strobus* were established on various soils in the beech and oak region during the 19th century (Pourtet, 1964); likewise in Austria during the same period (Rannert, 1958; Cieslar, 1901), and in Slovakia in 1809 (Holubcik, 1968a).

The first half of the 19th century in Germany brought such widespread planting and natural regeneration of eastern white pine in forests of all ownerships that the management of this tree was the subject of a special meeting of German foresters in 1833 at Strassburg. Foresters at this meeting proclaimed, "We all agree about the good silvicultural qualities of this exotic. But there are several perils: It looks as if a crisis always comes after 40 years of growth" (my translation from Hesse, 1954).

Half a century later the Union of German Forest Research Institutes made an inquiry concerning adaptation and other qualities of the eastern white pine. In answer, in 1883 a report was published by Weise (cited in Hesse, 1954), and it showed that the tree had proved to be well adapted to German ecological conditions--from East Prussia to the most southern parts of Germany. Its growth was good except in stands which had been established in the cooler climates of the higher mountains.

It is astonishing that damage and probable mortality due to the white pine blister rust (pathogen *Cronartium ribicola* J.C. Fisch. ex Rabenh., first found in the Baltic States in 1854 (Fassi, 1960)) was not mentioned in Weise's report; the disease was already three decades into its 30-year sweep across Europe (between 1865 and 1900, Mülder, 1954). Perhaps mortality was limited during that period. By 1926, however, losses were obvious and a second request for information was sent to 2,000

forest administrations and foresters in Germany and Austria. The result of this inquiry was presented at the meeting of the German Forestry Society 1927 at Frankfurt by Vanselow (1927). His conclusion was: The losses during youth and pole age caused by blister rust were so heavy that this excellent tree henceforth should be used only as a temporary nurse crop. Even more depressing was the opinion of Tubeuf (1927); he wanted the white pine completely replaced by the resistant *Pinus peuce* Griseb.

Fortunately, the white pines out in the European forests didn't know about their "First Class Funeral", as the proceedings of this meeting came to be called; they continued to grow. The continuing presence of the tree was an undeniable fact, and this led to the constitution of the "White Pine Commission," which visited the German regions where *P. strobus* was grown extensively. In its report (Wappes *et al.*, 1935), the Commission came to the following conclusions:

1. Blister rust was found in all stands that were inspected; together with the honey fungus it caused heavy losses.

2. The growth of the white pine was good on all sites.

3. Use of the tree was absolutely necessary to secure certain and easy reforestation on poor soils after coppice, and fairly complete removal of litter.

4. Given proper management, natural regeneration came on all soils.

5. The tree had a shallow root system; therefore it was not storm resistant.

6. Logs generally brought good prices, but the market possibilities for small material were limited.

After World War II reforestation problems again aroused the "White Pine Question". Another assembly of foresters discussed the problem for a third time, during the meeting of the Hessian Forestry Society in 1954. Three lectures on the problem were presented and published in the Society's annual report (Hesse, 1954; Mülder, 1954; Rossmässler, 1954). These discussions resulted in the firm belief that in the state of Hesse white pine would maintain its importance in forests of all ownerships.

DISTRIBUTION OF EASTERN WHITE PINE

The ups and downs in the evaluation of the place of *P. strobus* in European forestry makes it difficult to obtain estimates of the present stand area. According to Buchanan (1964) it is growing in more than 40 European countries, but we can be sure that the area in most of these countries is tiny. The most recent collection of stand data was reported for middle Germany by Lembcke (1966), for Austria by Rannert (1958, 1959a,b, and 1960), and for Hesse in 1954 by Eckstein (in press). While all these data are not fully comparable, those for middle-Germany and Hesse are listed, according to age classes, in Table 1. This helps correct estimates made before the war for Germany (Wappes *et al.*, 1935), and even those made earlier for Switzerland (Wappes, 1927).

Table 1. Hectares of *Pinus strobus* stands, as reported by Lembcke (1966) and Eckstein (in press)

	Age classes					
	1-20	21-40	41-60	61-80	81-100	41-100 (total)
Middle Germany (after Lembcke)	33.5	100.9	43.8	68.5	9.5	121.8
Hesse (after Eckstein)	72.4	137.4				1,003.2

The decline of the white pine area is evident. This corresponds with the situation in other countries (Beversluis, 1938; MacDonald *et al.*, 1957; Misson, 1962). In opposition to this are announcements of increased plantings in the Netherlands and Czechoslovakia (Gremmen, 1966; Holubcik, 1968a), plus my personal observations in Hesse, and other information from research workers of several European countries, for which I am indebted.

Considering these facts, my estimate is that the present (or at least recent) area of *P. strobus* in Europe may in fact be as great as shown in Table 2.

Table 2. Estimated European area of *Pinus strobus* in hectares

Country with at least 10 ha	Net area of fairly pure stands	Additional area of mixed stands with some *P. strobus*
Great Britain	20	--
Norway, Denmark, Sweden, Finland	10	--
Netherlands, Belgium, France	40	20
West Germany	5,050	18,000
Middle Germany	360	1,600
Poland	150	500
Switzerland	220	?
Italy	30	30
Austria	520	?
Europe	6,400	20,150 (1,600± net area)

The sum of 6,400 ha, with the addition of about 1,600 ha net area in the mixed stands, can only be expressed in ppm of the 136,000,000 ha of European forests. But things look different in Germany where the percentage of the white pine area is a little more (0.05%), and in Hesse where 0.2% is reached. In southern Hesse (Hesse-Darmstadt), between the rivers Main and Neckar, 1.3% of the forested area is occupied by white pine (Eckstein, in press). In one southern district (Forstamt) of Hesse-Darmstadt the area reaches 7.5%.

The statement of Buchanan (1964, p. 103), that in Austria there occur 750,000 acres of *P. strobus* (or almost 10% of the forested area), is nearly six hundred fold too high. Even if we consider only Upper Autria where more than nine-tenths of the Austrian white pines are growing, the percentage will scarcely reach 0.1 and not almost 10.

SILVICULTURAL QUALITIES OF EASTERN WHITE PINE

White pine has been planted over a wide range of European forest sites. It is well adapted to the warmer temperate region (Mondino and de Vecchi Pellati, 1960). However, in the northern boreal zone as well as mountainous regions of more than about 600 m above sea level it is maladapted; there the growth is poor and top breakage will occur after icing of the crowns and following heavy snowfall (Rohmeder, 1931; Rannert, 1959a,b). The tree has shown satisfactory growth on rocky slopes and good performance in wet bogs (Müller, 1937). Best development, however, is made on moist loamy sands (Badoux, 1929).

In Germany it has been used mostly to reforest impoverished soils after coppice, overgrazing, or where there are very acid soils due to presence of heather. Transplant stock 3 or 4 years old soon suppresses the heather and other weeds of these acid soils. Needles that are shed are rich in nutrients, and on warmer sites with sufficient moisture the litter decomposes easily. A good humus layer is formed (Rohmeder, 1931; Wappes *et al.*, 1935; Rossmässler, 1954). The improvement of worn out soils also affects growth of other species. Jentsch (1955) compared pure stands of Norway Spruce with others mixed with white pine. After 28 to 43 years the spruce in the mixed stands had grown the equivalent of more than one site class better than in the pure stands.

An intrinsic quality of *P. strobus* is its hardiness. It is not damaged by late frosts and therefore especially suited to frost localities (Ernst, 1954; Hengst, 1959; Misson, 1962; Eckstein, in press).

At places where no icing of the crowns occurs, the tree is markedly resistant to snowbreak (Vanselow, 1927; Rossmässler, 1954; Eckstein, in press). This contrasts with experiences from the cooler climate of higher regions.

Another valuable feature of this introduction is--astonishing for a pine--its tolerance. Tolerance is more pronounced in localities with good water supplies than in drier ones.

Natural regeneration is relatively easily obtained, provided the water supply is sufficient (Vanselow, 1927; Wappes *et al.*, 1935; Berard, 1958; Pourtet, 1964; Eckstein, in press). Spring droughts will kill tender seedlings on more arid sites.

These excellent silvicultural qualities are, however, partly offset by less desirable ones, as follows:

1. The tree develops a shallow root system and for this reason is unable to penetrate heavy soils. This may be the cause of the "crisis after forty years of growth" (Hesse, 1954). This confined root system often cannot support the tree, and windfall is not uncommon (Wappes, *et al.*, 1935; Penschuck, 1937).

2. The relatively high water requirement is another limiting factor. White pine develops poorly on the hot, dry slopes and ridges of the Rhenish Schist Mountain Range (Rüdesheim). The tree becomes dwarfed under more arid conditions (Misson, 1962).

3. Another limiting factor comes into play when the tree is planted in localities having a short growing season. The first sign of this problem is that there is no decomposition of litter--only raw humus is formed (Wappes *et al.*, 1935).

4. Serious enemies are game animals (Eckstein, in press). The honey fungus *Armillaria mellea* Sacc. (Rohmeder, 1957; Rossmässler, 1954; Rubner, 1925; Eckstein, 1966), and, of course, the blister rust (Mülder, 1960). Several *Pissodes* species heavily damage seedlings and stands of sapling and pole size (Eckstein, in press). Needle cast fungi are less important (Sperber, 1959).

5. In mixed stands and pure ones with open canopies the trees produce very little clear lumber (Hoemann, 1928). They must be pruned if good logs are desired.

GROWTH AND YIELD OF EASTERN WHITE PINE

P. strobus makes rapid height growth (Holubcik, 1968b). According to the yield table (Eckstein, in press), maximum growth is reached at the age of 15 to 20 years. It will outgrow all European forest tree species and keep a dominant position for more than 80 years. Figure 1 (from Eckstein) shows the height growth of the average sample white pine for 5 site classes, compared with growth of larch (*Larix decidua* Mill.) for site classes I and III, and of beech (*Fagus silvatica* L.) for site classes I, III, and V.

The number of stems per unit of area decreases rapidly with age. On the best sites, a fully stocked stand at age 80 years will consist of only 200 stems per ha (= 80 per acre). The average good-site tree will then have a 50 cm d.b.h., but if white pine is planted as a nurse tree on hot and dry slopes only 27 cm d.b.h. will be attained. Scotch pine requires 200 years to grow to these dimensions, and Norway spruce 140 years (Eckstein, in press).

The form factors of the stems are more than 10% better than those of Scotch pine, but the taper of larger trees is greater than that of Norway spruce (Eckstein, in press).

Given proper management, according to Eckstein (in press), white pine stands at age 80 have a basal area of from 26 to 40 square meters per hectare (= 110 to 170 square feet per acre).

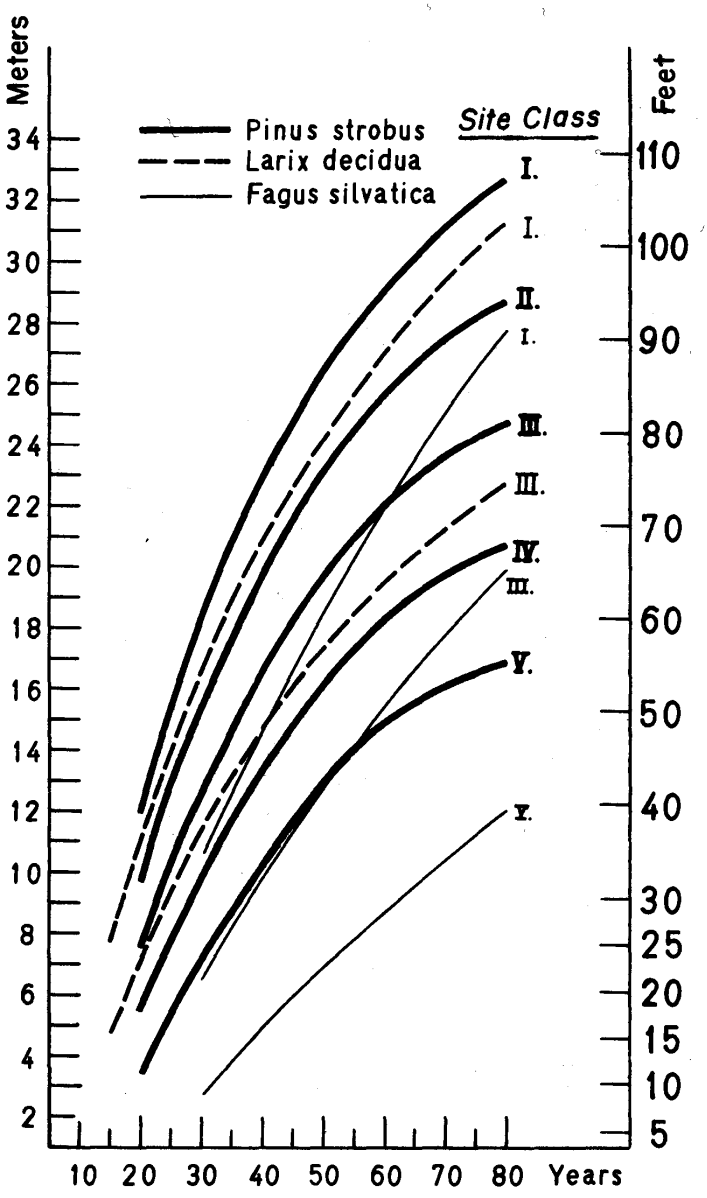


Figure 1. Average height of *Pinus strobus* on various sites, compared with that of *Larix decidua* and *Fagus silvatica*, Odenwald Mountains, state of Hesse, Germany (after Eckstein, in press).

Since in well managed stands the mean annual growth culminates at 55 to 70 years, rotations of 80 to 120 years seem desirable. This coincides with average rotation ages used in European temperate-zone forests.

Consequently, the total yield of eastern white pine--50% from thinnings--far surpasses that of all European forest trees. Figure 2 (also from Eckstein) shows the total yield of even aged stands on the rocky, sandy soils of the Odenwald Mountains, compared with Scotch pine and Norway spruce. The three conifers are introductions in this old beech-forest country.

OTHER WHITE PINES

Among the other white pines *Pinus griffithii* McClell. (syn. *P. wallichiana* A. B. Jacks.) has been planted in some stands in the southern Odenwald Mountains and near the Baltic Sea in northern Germany (Schenk, 1939). The tree never has approached the growth of eastern white pine and it has not proved to be hardy enough under the average middle-European climatic conditions. Stands in the Odenwald Mountains were mostly killed by frost in the winter of 1946-47 (Rossmässler, 1954). Cieslar (1901) thought it useful for the southern parts of Europe. Vivani (1962) reports a test with 9 provenances of this Himalayan white pine and mentions the poor timber form of this tree.

CONCLUSIONS

Eastern white pine has been grown in European forests for more than two centuries. It proved to be essential for reforestation aimed toward recovering impoverished soils. Besides this, the attributes of eastern white pine for contributing to increased growth of other conifers in mixed stands, as well as of deciduous trees (growth of "the poplar between the conifers", Wappes, *et al.*, 1935), is so important that the species' overall qualities more than balance its weak points.

If we could succeed in controlling blister rust, eastern white pine would become one of the most important trees of the European forests.

SUMMARY

Since the European forests are composed of relatively few tree species, early attempts were made to enrich them with fast-growing exotics. One of the first to be introduced was eastern white pine (*P. strobus*). This tree showed good qualities and proved to be well adapted to the climate of the deciduous forest zones of western Europe, especially in the warmer parts having a more continental climate.

In this region eastern white pine is completely hardy, withstands late frosts, grows on difficult soils, and is easily regenerated naturally. It is a half-tolerant tree and especially adapted for competing in mixtures with hardwoods. The dead needles enrich devastated soils and keep weeds down. Stem forms are good and the growth is excellent; in fact, no European forest tree will bring a higher yield on any site.

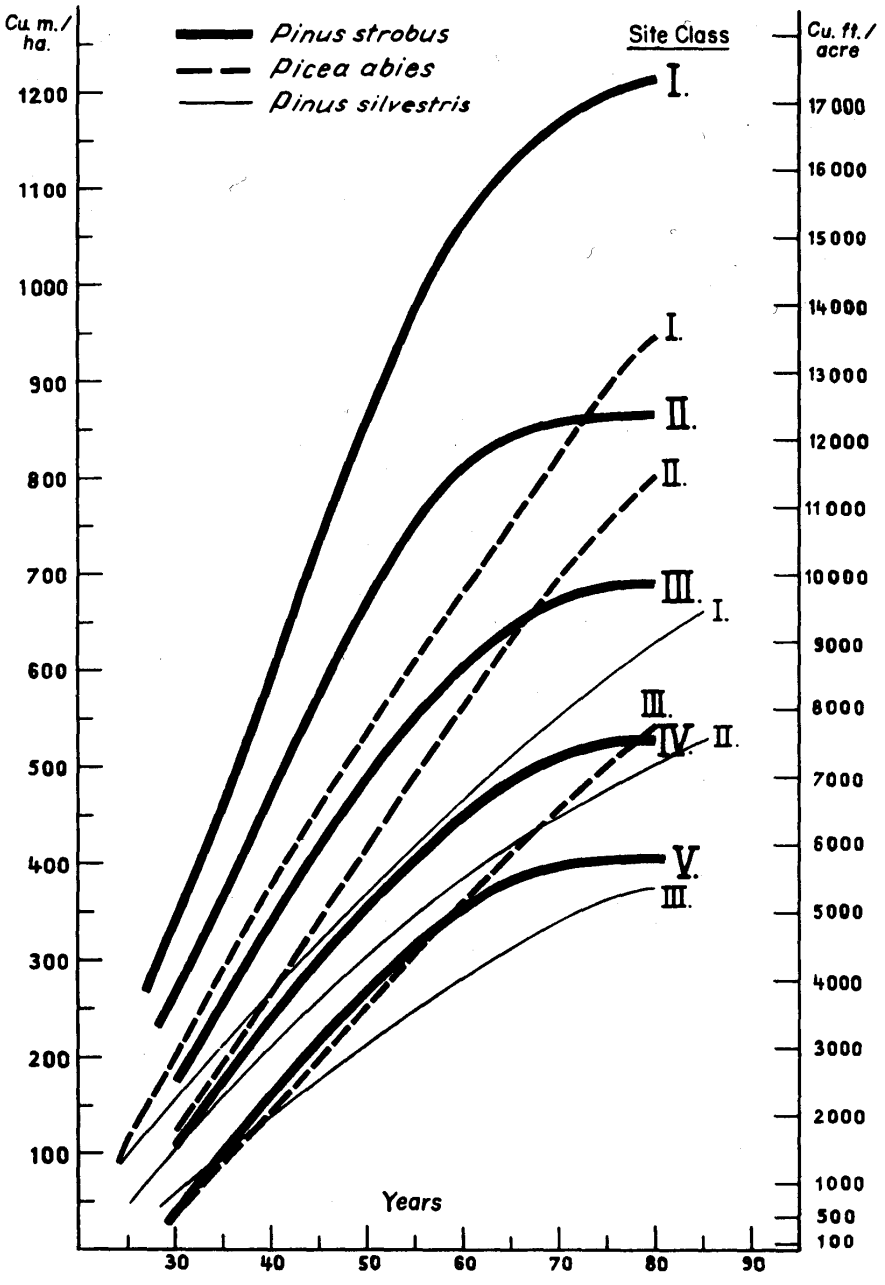


Figure 2. Wood yield of *Pinus strobus* on various sites, compared with that of *Picea abies* and *Pinus silvestris*, Odenwald Mountains, state of Hesse, Germany (after Eckstein, in press).

It is heavily damaged by game animals, by the honey fungus, and by the white pine blister rust.

The European area of *P. strobus* may be estimated to 6,400 ha, most of it in West Germany with a center in Hesse, middle Germany, and in Austria. Moreover it is found in mixed forests of more than 20,000 ha. In the last decades the establishment of new stands of this valuable tree was curtailed because of the threat of blister rust.

The introduction of the eastern white pine to higher mountains of more than 600 m above sea level has been a failure; there the tree shows poor growth and is heavily damaged by ice breakage.

Introductions of other white pines are negligible. *P. griffithii* is not hardy enough in northern and central Europe, but perhaps will grow in warmer parts. *P. monticola* proved to be as slow growing as *P. peuce*, under average European conditions.

ACKNOWLEDGMENTS

For providing valuable information on distribution, performance, and size of eastern white pine stands in Europe, I am indebted to Dr. H. Bryndum, Denmark; Dr. O. Dittmar, Germany, Dir. B. Fassi, Italy; Doz. M. Holubcik, Czechoslovakia; Dr. K. Holzer, Austria; Dr. R. Immel, Germany (for Spain and Portugal); Research Asst. P. Krutsch, Sweden; Prof. R. Morandini, Italy; Dr. J. Parde, France; Dr. G. Pollanschütz, Austria; Dr. S. Smelko, Czechoslovakia; Ing. A. Thill, Belgium; Ir. P. G. de Vries, Netherlands.

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FLOOR DISCUSSION

Moderator Bingham withheld discussion on the previous paper by Dr. Kurt Holzer until after Dr. Hans Hattemer (substituting for Dr. Richard Schmitt due to his illness) read Dr. Schmitt's closely related paper. Discussion on both papers follows.

HEIMBURGER: I want to ask Dr. Holzer, what is the lime requirement for *Pinus peuce*? In Canada we have found that *P. peuce* cannot tolerate acid soils as well as *Pinus strobus*. *P. peuce* can grow moderately well on acid soils, but it grows very well in calcereous soils. In your paper you mentioned the very calcereous soils of the Alps and other places.

HOLZER: It is reported in the literature that *P. peuce* is grown only on basic soils. I think Dr. Vidakovic, from Yugoslavia, might be able to answer more completely.

HEIMBURGER: I see. So it checks with your observation. It cannot stand acid soils. It needs fairly neutral soils.

VIDAKOVIC: I don't know too much about *P. peuce* because it occurs well to the south of my station, in the state of Macedonia. However, I have been in Macedonia, and I know the people working with *P. peuce*. I remember once in a discussion with Bozidar Nicota, Director of the Forestry Institute in Skopje, he told me there are *P. peuce* stands growing on acid soils, but in very small patches. Nicota was of the opinion that maybe there are two types of *P. peuce* in Yugoslavia. I have seen *P. peuce* in the Pelister Mountains on calcareous soils. It's from Nicota that I understand that in Macedonia there's a type growing on acid soil too.

HEIMBURGER: The seed dealers in North America supply most of the *Pinus griffithii* seed--from northern Italy. What we would like to know very much is how *P. griffithii* behaves in northern Italy.

DUFFIELD: I have seen *P. griffithii* in two general situations in northern Italy. I did not travel extensively there, but in one area where the species is famous in Yugoslavia (formerly an Italian area, where the species was planted by the Italians) it is on somewhat acid soils growing with *Quercus rubra* and the two species are doing very well together. Further to the east around Trieste, it's growing very well on calcareous soils, and the experience there is that it does better than *P. strobus*

on these soils. *Pinus griffithii* is grown and bred on difficult sites. It's rather common as an ornamental in the lower Po River valley where it reaches 40 feet tall, then begins to break down. The breakdown may be due to inadequate soil drainage; soils involved are rather unsuitable.

WICKER: I have a question for Dr. Holzer. In one of your slides you showed a small pine growing at high elevation, with a needle cast. Do you know the cause of this needle cast; is it climatic or biotic?

HOLZER: It's a fungus infection, *Lophodermium*.

CALLAHAM: I have only seen *Pinus strobus* and *P. griffithii* in northern Italy through very fog-shrouded, rainy climates. Around Lake Maggiore and Lake Como both species grow very well around the old villas where planted as ornamentals. These are the sources of the seed that Emma De Vecchi reported as being spontaneous *P. strobus* x *P. griffithii* hybrids. They are being used extensively in planting programs by the Burgo Company in Turin.

BINGHAM: I have a question for Dr. Holzer. Is there any pattern in the growth of *Pinus cembra* from the eastern distribution in Rumania vs. growth of the western distribution in France?

HOLZER: No materials exist in my tests; only elevational materials.

BORLAUG: I would like to ask Dr. Holzer how frequently it is that you find individual *P. cembra* seedlings with much greater growth? In your slide there were a couple of seedlings--presumably of the same age--that were 2 or 3 times as tall as the others. Is this a frequent occurrence?

HOLZER: The slide in question showed a trial of progenies of selected trees from several stands. Here we found that progenies of several mother trees gave different growth. This is as much as we know at present, except that there is altitudinal differentiation within the same stand. Only time will tell.

DE JAMBLINNE: I would like to know if there is increased blister rust resistance of *Pinus strobus*, through some silvicultural treatments in Germany.

HATTEMER: I haven't heard anything about that; nor is it covered in Dr. Schmitt's paper.

DUFFIELD: I don't know whether anybody can answer this, but it struck me that *Pinus monticola*'s reputation in Europe is not nearly as good as it might be. Is there any knowledge at all of the provenances used?

HOLZER: I have no knowledge of the provenances involved in the few *P. monticola* plantings I covered.

DUFFIELD: Yet we have very different races of *P. monticola* with which to breed.

WHITE PINES OF ASIA: *PINUS KORAIENSIS* AND *PINUS ARMANDII*

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ABSTRACT

Pinus koraiensis is a straight-boled tree with a pyramidal crown. It can attain 300-500 years of age, around 40 m in height and 1.50 m in DBH. It ranges through Korea and eastern Manchuria into southeastern Siberia, with outliers on the Japanese islands on Honshu and Shikoku. It occurs on the transitional zone from the northern temperate to subarctic forest zone. On the north it withstands severe winter cold, as low as -35°C. But it also thrives in the rainy-summer region of the south, on deep humus-rich sandy loam of weak acidity. Some forms are also adapted to rocky slopes, as well as to relatively shallow and dry soils of south-to-west-facing slopes.

The seed needs stratification and the seedlings behave as shade tolerant, gradually turning to intolerant as they become older. Artificial plantations are successful anywhere in the temperate forest zone, even at elevations as low as 100 m above sea level. No serious pest damage has been recorded either in nurseries or plantations. However, some young plantations in limited areas have been damaged by blister rust.

The average tree in natural stand acquires a DBH of 17 cm and a height of 13 m in 50 years. A plantation on a good site, however, acquires, on an average, a DBH of 28 cm and a height of 23 m at the same age, producing an average stand volume of 350 m^3 per hectare. The wood is characterized by light yellowish brown sapwood and yellowish brown heartwood. It is straight-grained, soft, moderately light, and moderately weak in bending and compression. With relatively low shrinkage, it is easy to kiln dry and easy to work.

Pinus armandii is a tree reaching 20 m in height, with wide-spreading horizontal branches. It ranges through western and southwestern China extending to northern Burma, extreme north-eastern India and southeastern Tibet. It also appears in Taiwan and Hainan. All of its habitats fall within the rainy-summer climatic type. It requires a much milder climate than does *Pinus koraiensis*. It is adapted to a wide range of soil moisture and acidity conditions, through semi-arid and alkaline to moist and acid soils. The ease in obtaining natural regeneration indicates a similar ease of artificial planting, although planting is uncommon.

The average tree in natural stands in Taiwan acquires a DBH of 25 cm and a height of 15 m in 50 years, thus showing a better growth potential than natural stands of *P. koraiensis*.

The wood properties are in general similar to those of *P. koraiensis* being heavier, stronger in physical strength and higher in durability than the wood of *P. strobus*.

PINUS KORAIENSIS SIEB. & ZUCC. (KOREAN PINE)

RANGE AND FOREST TYPE

The natural range (Fig. 1) of *P. koraiensis* covers northeastern Korea from 39°N latitude, and extends into Manchuria through Kirin, Heilungkiang, and Primorskays up to southeast Siberia around 54°N latitude. It occurs sporadically on high mountains in south Korea and in central Honshu and Shikoku of the Japanese islands (Critchfield and Little, 1966).

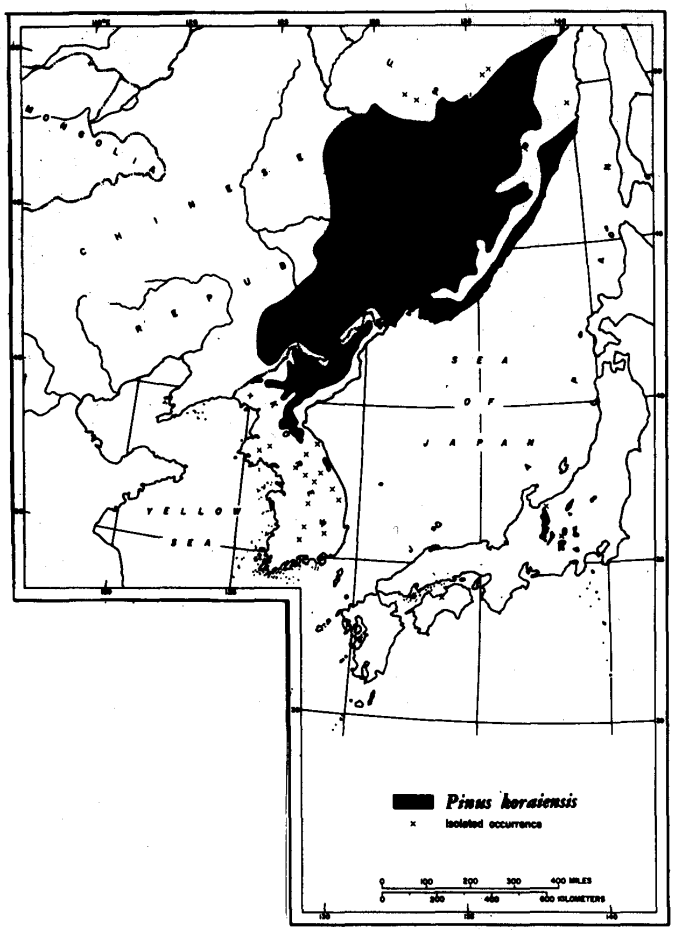


Figure 1. Natural range of *Pinus koraiensis* (reproduced from Critchfield and Little, 1966).

The vertical range of *P. koraiensis* on the mountains of Korea is shown in Fig. 2 (Chung and Lee, 1965). *P. koraiensis* occurs above the deciduous oak belt in the transitional zone from the northern temperate to subarctic forest zone (Uyeki, 1932). In the northern temperate forest zone it starts to appear mixed with *Quercus mongolica* Turcz. and *Abies holophylla* Maxim. forming a *P. koraiensis-A. holophylla-Q. mongolica* forest type. The components other than these 3 major species are linden (*Tilia amurensis* Rupr.), birch (*Betula costata* Trautv.), walnut (*Juglans mandshurica* Maxim.), ash (*Fraxinus rhynchophylla* (Hance) Hemsl.), elm (*Ulmus mandshurica* Kakai.), and kalopanax (*Kalopanax pictus* (Thumb.) Kakai.). Further north in latitude and higher in elevation, *A. holophylla* and *Q. mongolica* are gradually replaced by *Abies nephrolepis* Maxim. Finally the range is taken over by the *Picea jezoensis* (Sieb. & Zucc.) Carr.-*A. nephrolepis* type which is the typical subarctic forest.

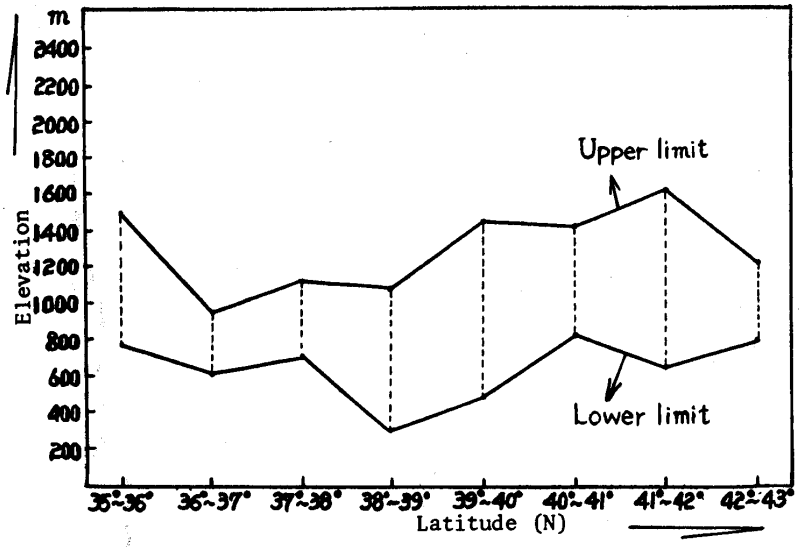


Figure 2. Vertical distribution of *Pinus koraiensis* in Korea.

Occasionally *P. koraiensis* forms small pure stands on west- to south-facing slopes where the soil is relatively shallow and dry, but commonly it forms a mixed forest type with *Abies* or *Quercus* (Fig. 3).

So far there is no evidence to show the presence of races of *P. koraiensis*; however, variants are on record. Dr. Uyeki (1925) reported a variant which he named *Pinus heterosuberosa*. It had a peculiar bark with transverse suberous bars 6 to 10 cm in length scattered on the whole surface at intervals of 6 to 10 cm. Dr. Uyeki found one plant of this variant on Mt. Kumkang of Korea. A dwarf variant was found in a plantation located in Kangwondo province. This tree was only 10 m tall and 22 cm thick at an age of 100 years. No natural hybrids are known to exist, but *P. koraiensis* has been successfully crossed with *P. lambertiana* Dougl. (Duffield and Righter, 1953).

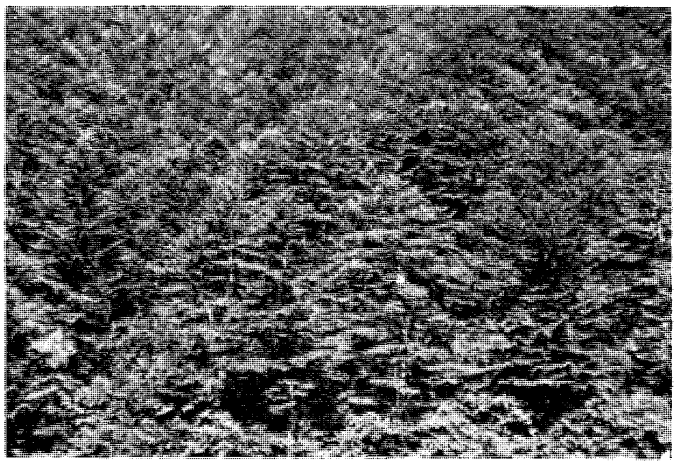


Figure 3. Outlooking view of the *Pinus koraiensis-Abies holophylla* forest type (Elev. 600 m, Mt. Sorak, 38°N lat.).

SITE REQUIREMENTS

The climate over the range of Korean pine is cool and humid. The mean annual temperature over the range in Korea is between 1.3°C and 7.5°C. The mean maximum temperature in August ranges between 23°C and 28°C and the mean minimum temperature in January ranges between -10°C and -25°C. The extreme low temperature during the winter over the range in Korea falls between -20°C and -35°C.

The annual precipitation over the range in Korea varies from about 700 mm in northern Korea to about 1,400 mm in southern Korea. Over 50% of the annual precipitation pours during the summer, 20% in the autumn, and around 6% in the winter (Fig. 4). Throughout the range in Korea, the precipitation is about 1 to 1.5 times the evaporation, and the mean annual relative humidity ranges from 70 to 75%.

While the low temperature limit of the natural range indicates the low temperature limit for artificial planting, the high temperature limit of the natural range does not indicate at all the high temperature limit for planting. Actually, plantations of *P. koraiensis* are successful in many areas in south Korea where the winters are much milder than in its natural range.

Soils within the range of Korean pine are derived from basalt, granites, gneisses, schists, and limestones, and less commonly from slates and shales. The soil profiles show various degree of podsolization according to the climatic condition at the site ranging from a weak podsolized brown forest soil in south Korea to a fairly podsolized acid brown forest soil in northern Korea. Korean pine grows on a wide range of soil texture from a light volcanic ash to a heavy clayey soil, but it prefers well drained sandy loams.

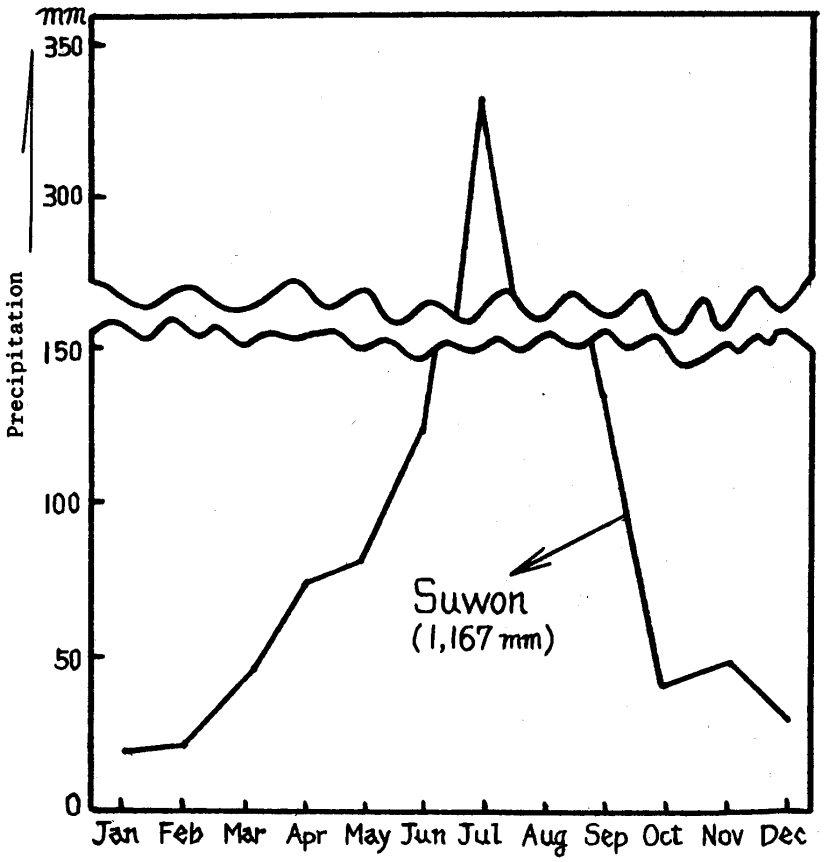


Figure 4. Monthly distribution of precipitation in Korea.

At many places within its range, site quality has been related to combinations of soil and topographic characteristics such as texture and thickness of the A- and B-horizons, topographic position, slope percentage, and aspect. The thickness of the A-horizon has the greatest influence on the rate of growth. High total exchangeable bases and high content of total nitrogen and organic matter also favor growth. However, within its natural range, *P. koraiensis* is the dominant component only on west to south facing slopes where the soil is relatively shallow and dry (Fig. 5).

In plantations, *P. koraiensis* is recommended for planting on slopes not favorable for larch or fir due to the relatively shallow and dry soil conditions.

North of the 38° parallel, *P. koraiensis* grows at elevations above 300 m; in the middle part of Korea, around 36° to 38° parallel, it grows in a band along the mountains between 600 m and 1,200 m above sea level. South of the 36° parallel it grows in the mountains at elevations higher than 700 m. However, *P. koraiensis* is being planted with good success practically everywhere in South Korea above 100 m provided the soils have not eroded and the drainage is good.



Fig. 5. *Pinus koraiensis-Pinus densiflora* Sieb. & Zucc. forest type on a dry west facing slope (Elev. 1,500 m, Mt. Chii, 35°N lat.).

SILVICULTURAL CHARACTERS

P. koraiensis is typically a pyramidal straight tree around 40 m high and 1.50 m d.b.h. at 300 to 500 years. It is known as the finest tree of Korea for timber quality. Leaves are dark green, straight, and 6 to 12 cm long. Cones are short-stalked and 9 to 14 cm long. The bark is thin, except on old trees, reddish grey, and smooth or dividing into scaly plates (Fig. 6).

Natural stands of *P. koraiensis* have served as a very important timber source of north Korea and Manchuria. This species also produces nuts and in many instances pine nuts are a good source of income.

It is a shade-tolerant tree when it is young, but gradually becomes intolerant as it grows.

P. koraiensis starts to bear cones at about 15 years but does not become a good producer until about 30 years of age. Although some cones are produced almost every year, abundant seed crops are produced only at intervals of 2 to 3 years. The seeds are large (1,080/l or 950/lb) and heavy with no wings; consequently, they are not carried great distances by wind. But seeds are often buried by rodents and birds at considerable distances from seed trees. The seeds exhibit embryo dormancy which can be broken by cold stratification. Although the rate of germination of stratified seed is as high as 64%, natural regeneration is difficult due to the destruction of seed by rodents and birds (Uyeki, 1925).

Artificial planting, however, is very successful anywhere in Korea except the coastal low land. Planting stock is obtained by sowing seed at the rate of 0.59 l/m^2, preventing rodent and bird damage, shading with



A. B.

Figure 6. Form of bark of *Pinus koraiensis* on A) 100-year-old tree from a natural stand on Mt. Sorak and B) 40-year-old tree from a plantation at Kwangyang.

lath during the first summer, and thinning to 400 seedlings/m^2 of seed bed in the fall. The stock is removed from the seed beds as 2-0 seedlings between 12 and 15 cm tall.

The form and distribution of the root system varies with the soil characteristics. It has several (usually three to five) large roots stretching downward and outward in the soil giving the tree a firm anchor under most conditions. No serious root damage in the nursery or in plantations has so far been recorded, except a slight amount by cutworms in the seed beds.

The common practice is to plant 2-0 or 2-1 seedlings at a spacing of 2 m. Growth is rather slow during the first 3 to 5 years after planting, but it gradually improves and thinning is needed by 20 years. Fifty to 80 years is the usual rotation for producing saw timber. Due to very poor self-pruning, a regular pruning practice is needed for production of knot-free logs (Fig. 7).

With regard to pests and disease, the black tipped sawfly (*Acantholyda posticalis* Mats.) has caused some damage in a middle-aged plantation (Lee and Cho, 1959).

Blister rust damage was first reported in 1937 (Takagi, 1937) in an 8-year-old plantation in Kyunggido Province of Korea. Takagi reported that around 650 planted stocks expressed blister rust symptoms on their

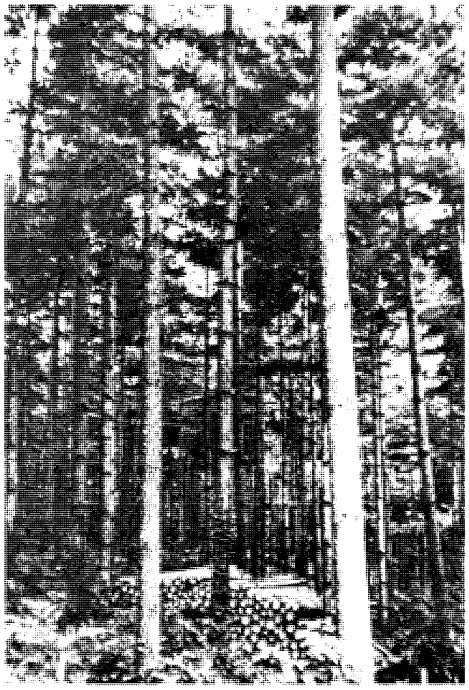


Figure 7. A thinned plantation of *P. koraiensis* 40 years old.

stems. The rust was identified as *Peridermium strobi*, the aecial stage of *Cronartium ribicola* J. C. Fisch. ex Rabenh. by Professor Hiratsuka (Takagi, 1937). Dr. Takagi failed to find any *Ribes* spp. around the plantation.

Forest pathologists of the Forest Experiment Station of Korea recently reported (not published) damage to a *P. koraiensis* plantation by blister rust in Kangwondo Province. Plantations 5 to 9 years old and 60 ha in total area located in 3 different sites in Pyongohang County, Kangwondo Province were damaged by blister rust (Fig. 8, 9, and 10). The pathologists reported that 35% of the planted trees were seriously damaged by this disease. However, no blister rust was found in a nearby 15-year-old plantation during 3 years of continuous observation. So far they also failed to find *Ribes* spp. growing around the infected area.

GROWTH PERFORMANCE

Growth in the natural stand is quite slow, probably because of cold climate and dry soil. It takes 5 to 30 years to come up to a breast height according to the site condition. Average growth performance of single trees in a natural stand growing on rocky shallow soil is given in Figs. 11 and 12.



Figure 8. Aecia of *Cronartium ribicola* on *Pinus koraiensis* at the base of the stem.



Figure 9. Aecia of *Cronartium ribicola* on the stem and branches of a *Pinus koraiensis* seedling.

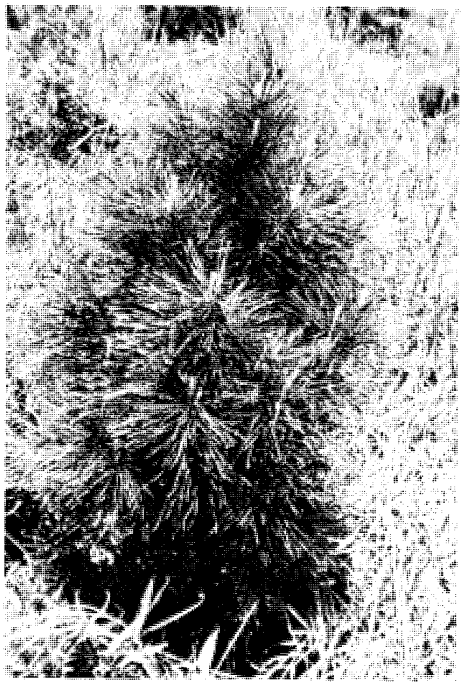


Figure 10. Witch's broom form of a *Pinus koraiensis* seedling infected by *Cronartium ribicola*.

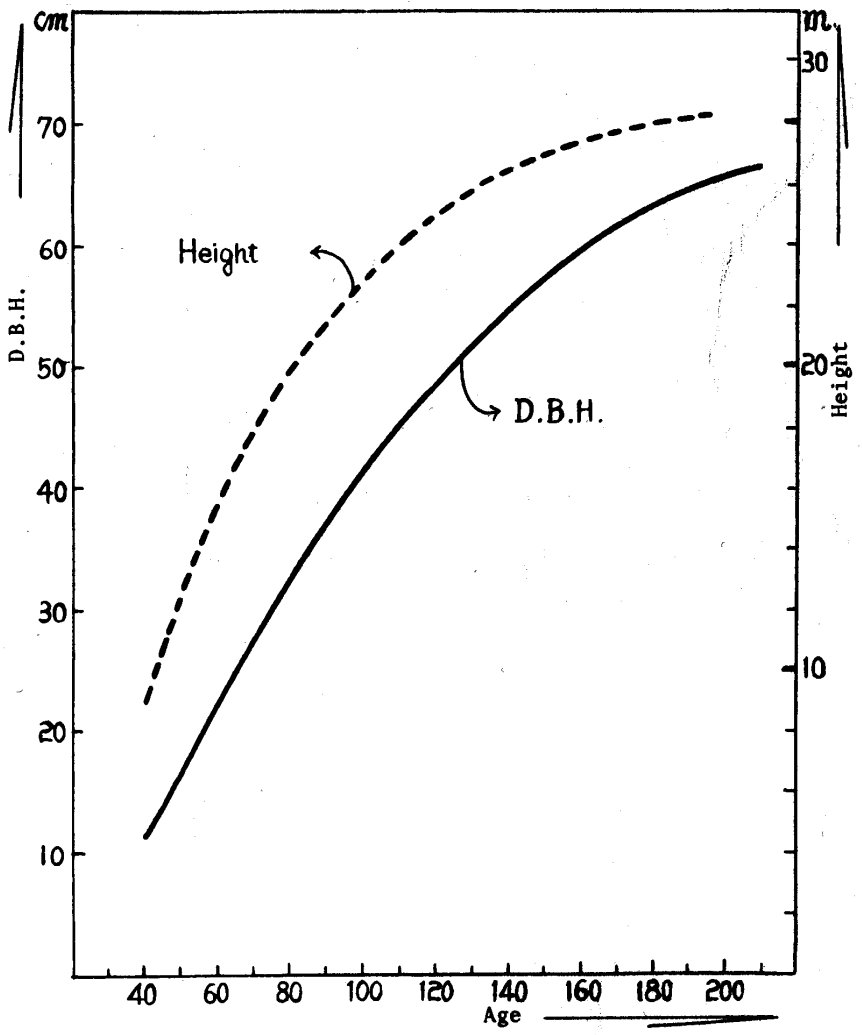


Figure 11. Height and diameter growth based on a single tree of *Pinus koraiensis* in a natural stand in northern Korea.

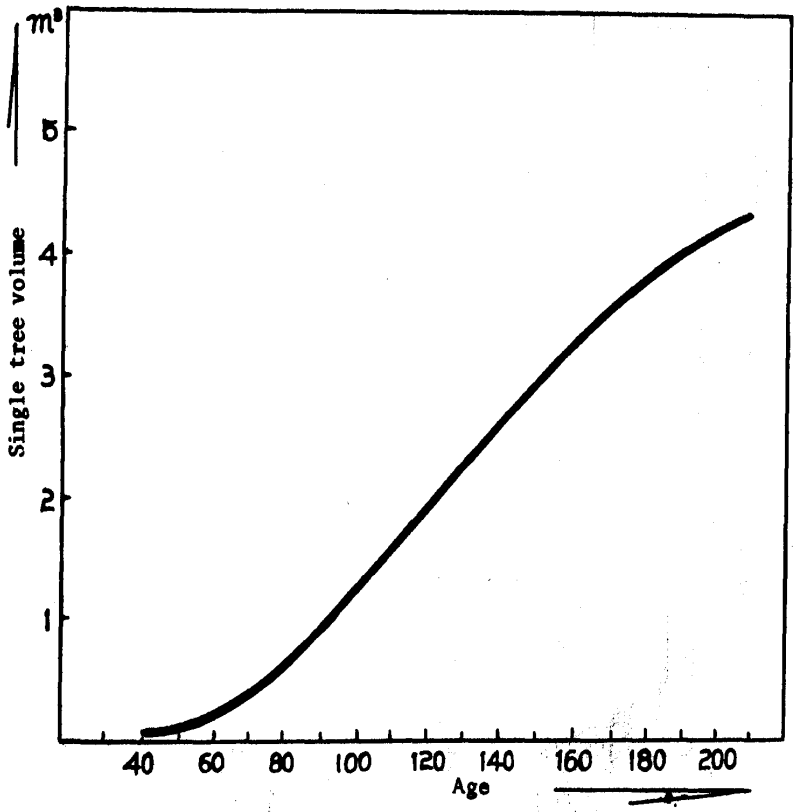


Figure 12. Volume growth based on a single tree of *Pinus koraiensis* in a natural stand in northern Korea.

According to studies on the yield and growth of *P. koraiensis* in which 103 plantations on various sites of south Korea were investigated (Kim and Lee, 1966), this species attains a size of 28 cm d.b.h. and 23 m of height in 50 years on a good site, giving a stock volume of 350 m^3/ha. The mean annual increment and the current annual increment curves culminate at the ages of 42 and 27 years respectively (Fig. 13-17).

TIMBER QUALITY

P. koraiensis is characterized by straight stems, light yellowish-brown sapwood, and a yellowish-brown heartwood which is easily distinguishable from sapwood. It is straight grained and medium to coarse textured. Resin canals are conspicuous, and located axial and radial, but the wood has no characteristic resinous odor or taste. Growth rings are distinct, and transition from springwood to summerwood is abrupt. Wood rays are fine and visible to the naked eye (Fig. 18). The average cellulose content of fiber is around 54.08% (α-cellulose = 70.68%) (Chosen Govt.-Gen., 1940).

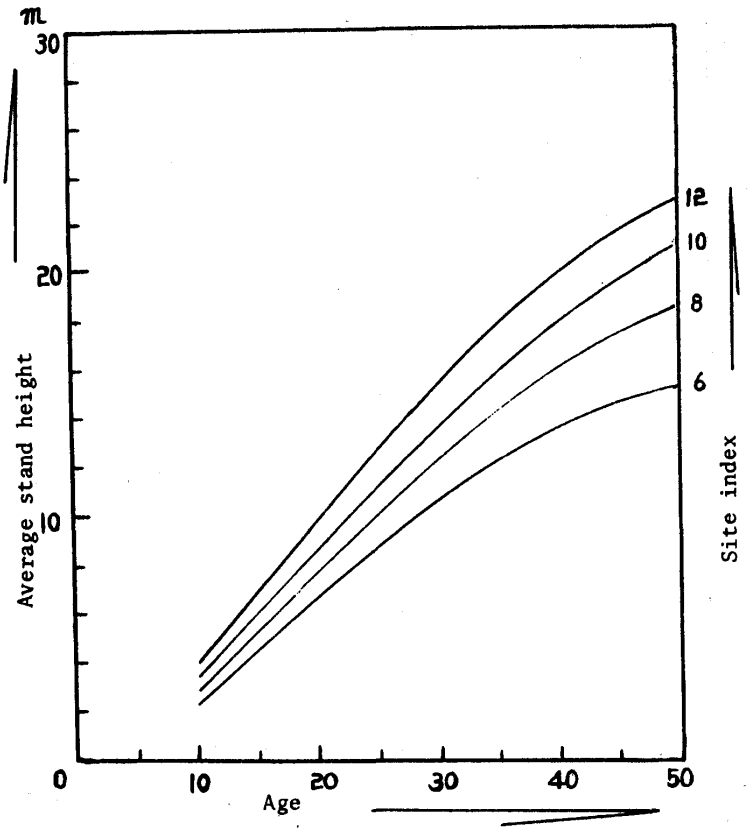


Figure 13. Relation between age, site index and average height for a well stocked stand of *Pinus koraiensis*.

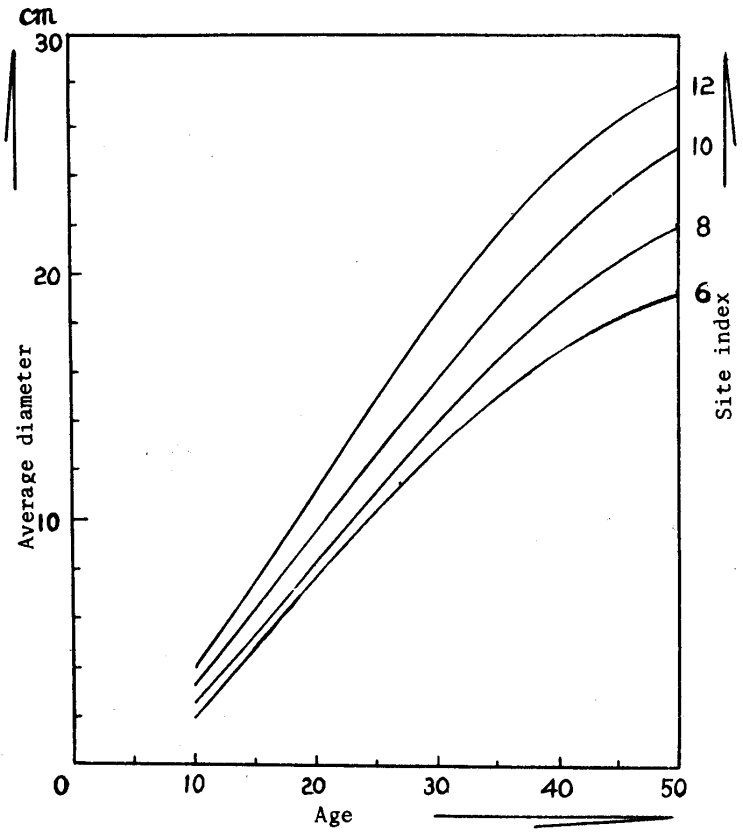


Figure 14. Relation between age, site index and average diameter for a well stocked stand of *Pinus koraiensis*.

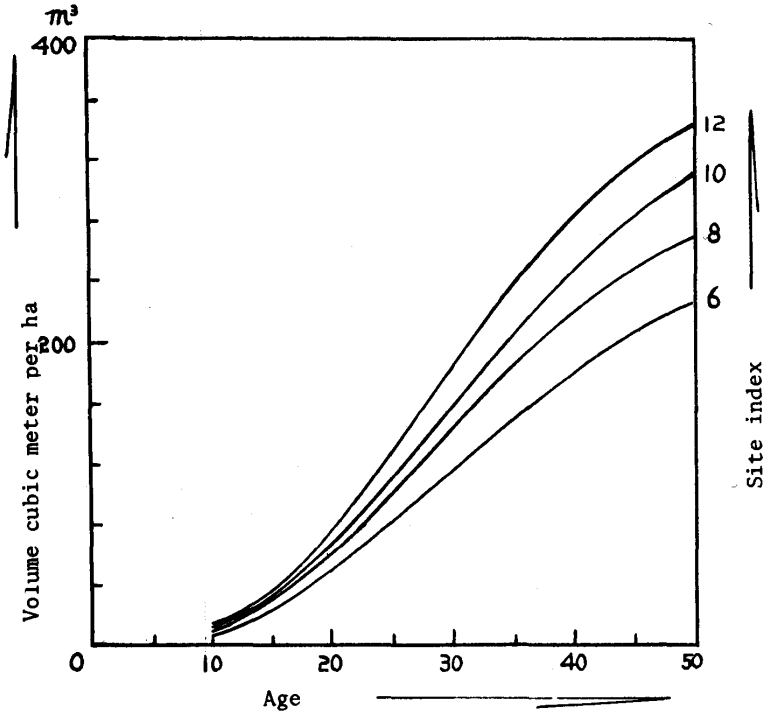


Figure 15. The volumes in cubic meter on age by site index for average well stocked stands of *Pinus koraiensis*.

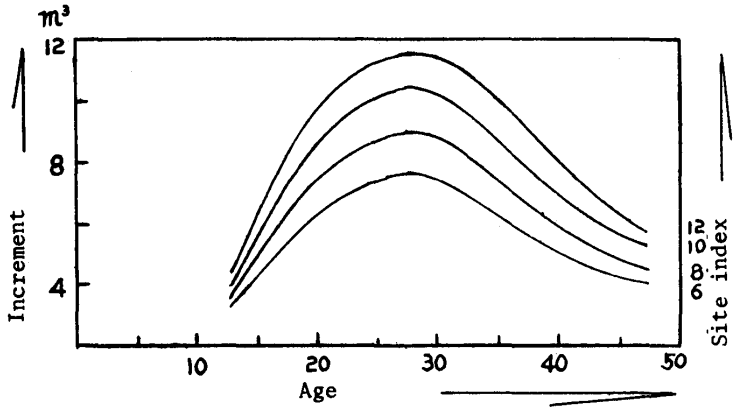


Figure 16. Current annual increment curve of major trees (volume per ha in cubic meters) of *Pinus koraiensis*.

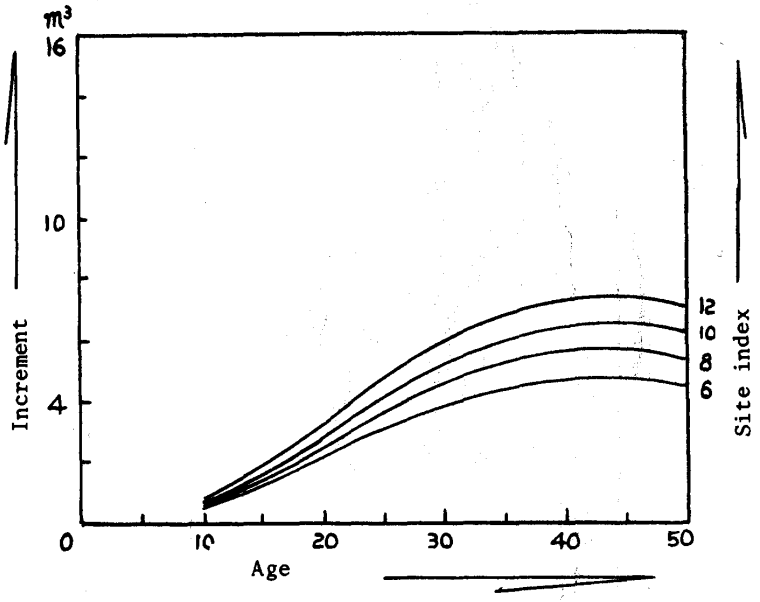


Figure 17. Mean annual increment curve of major trees (Volume per ha in cubic meters) of *Pinus koraiensis*.

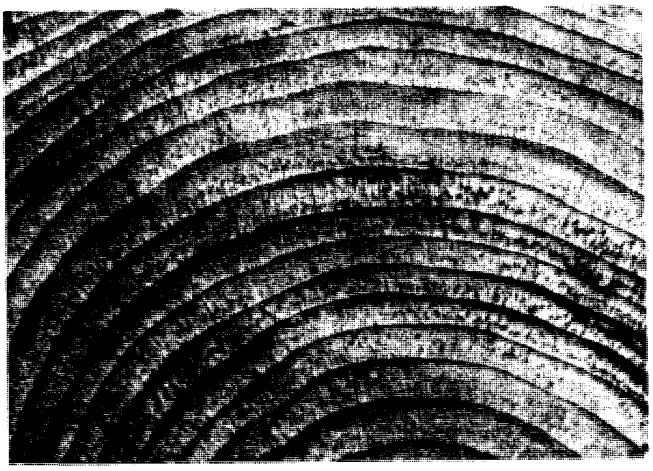
The wood of *P. koraiensis* is moderately light with specific gravities of 0.49 (air dry) and 0.45 (oven dry). It is compact and soft, moderately weak in bending (551 kg/cm^2), compressive (321 kg/cm^2), tensile (451 kg/cm^2) and shearing (62 kg/cm^2) strengths (Chosen Govt.-Gen., 1940).

With a shrinkage of 2.3% in the radial plane, 6.3% in the tangential plane, and 8.9% in volume the wood is easy to kiln dry and stays in place well after seasoning. It is easy to work with tools and less tortured than any other native pines in Korea. It is rated as fairly durable in decay resistance. It takes paints and polish well (Kishima, Okamota, and Hayashi, 1962). The wood is used principally for construction and furniture.

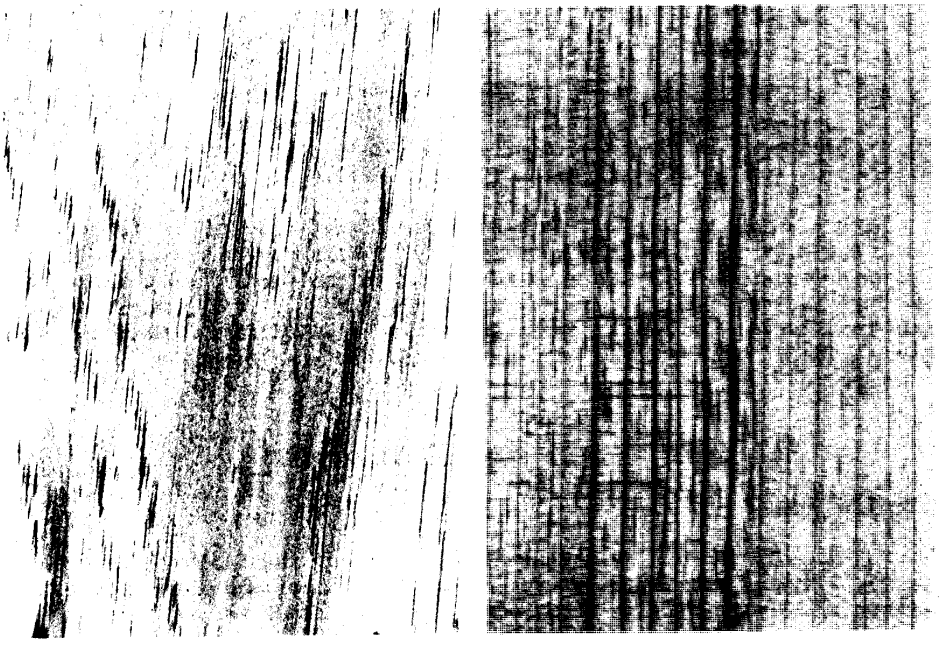
PINUS ARMANDII FRANCH. (ARMAND PINE)

RANGE AND FOREST TYPE

P. armandii is wild in the mountains south of the Yellow River in central, western, and southeastern China, from Shensi and Kansu south to Szechwan and Yunnan ranging from 34°N to 35°N latitude and west to northern Burma, extreme northeastern India, and southeastern Tibet (Fig. 19). It also occurs in Formosa. On the mainland of China, at around 24°N latitude in the southwestern Chinese province of Yunnan, or at around 30°N latitude in the central-western Chinese province of Szechwan, *P. armandii* usually occupies rocky sites at 2,300 to 3,300 m above sea level. The altitudinal range drops to 1,200 to 2,000 m above sea level in the provinces of Kansu and Shensi around 34°N



A.



B. C.

Figure 18. A) cross section, B) radial section, and C) tangential section of *Pinus koraiensis* wood.

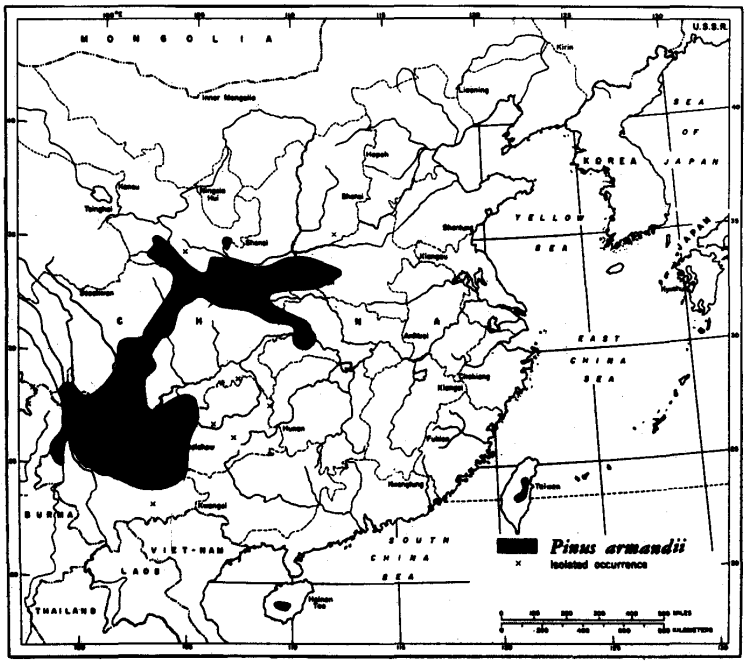


Figure 19. Natural range of *Pinus armandii* (reproduced from Critchfield and Little, 1966).

latitude. In Formosa it appears at a high altitude, between 2,300 m and 2,800 m above sea level, in the central mountain ranges between 23°N to 24°30'N latitude. It appears at a high elevation in Hainan, around 18°30'N latitude.

On the mainland of China, it is a component of the mountain coniferous forest of the southwestern plateau occurring mixed with spruce, fir, and hemlock. On Formosa (Fig. 20) it appears occasionally as scattered stands in the grassland but commonly it appears in a mixed forest with Taiwan spruce, Chinese hemlock, and Taiwan red pine. The primary components of the forest besides Armand pine are *Picea morrisonicola* Hayata, *Tsuga chinensis* (Franch.) Pritzel, *Pinus taiwanensis* Hayata, *Cyclobalanopsis morii* (Hayata) Schottky & Kudo, *Chamaecyparis obtusa* var. *formosana* (Hayata) Rehder, *Chamaecyparis formosensis* Matsumura, and *Juniperus formosana* Hayata. *Taiwania cryptomerioides* Hayata, *Cyclobalanopsis stenophylloides* Masamune, *Rhododendron formosanum* Hemsl., *Lithocarpus amygdalifolius* (Skan) Hayata, *Malus formosana* Kawakami & Koidzumi, *Trochodendron aralioides* Sieb. & Zucc., *Ulmus uyematsui* Hayata are the minor species.

One variety, *P. armandii* var. *amamiana* (Koidz.) Hatushima, was found on Yakushima (300 to 500 m above sea level) and Tanegashima (150 m above sea level), the southmost islands of Japan, around 30°N latitude (Hatushima, 1938). It is distinguished from *P. armandii* by short, stiff leaves and ovoid cones. The fertility of seed is very low in this habitat. This variety appears at a lower elevation in the Japanese islands than does the main species in China and Formosa.



A. B.

Figure 20. A) Outlooking view and B) inner view of a *Pinus armandii* forest, Mt. Alishan, Taiwan (photo by Mr. J.-C. Liao).

No natural hybrids are known to exist but *P. armandii* has been successfully crossed with *P. lambertiana* (Duffield and Righter, 1953).

SITE REQUIREMENTS

Pinus armandii requires much milder climate than *P. koraiensis*. The habitat in the mainland of China has quite a mild winter and averages over 200 days of frost-free growing season. Annual precipitation ranges from 500 mm in the northwest (Kansu) to 1,100 mm in the south (Yunnan) with a peak rainy period in June and July (Fig. 21). It appears that the major part of the natural range belongs to a semi-arid climate type. Temperature data for the Chinese mainland and Formosa habitats are given in Fig. 22.

The soils over the natural range of *Pinus armandii* on the Chinese mainland are derived from limestone in many cases, but some are derived from shale, slate, and sandstone (Szechwan and Yunnan). Neutral to alkaline soils are commonly found in arable flat lands, although in high elevations in Kansu and Shensi, degraded Chestnut-soils and Chernozems are developed. In Szechwan a brown forest soil type is developed on the shale, slate, or sandsone. Elsewhere, with more rain, podsolization has progressed to form red and yellow podzolic soils and some Rendzina type soils (Mima and Kato, 1938).

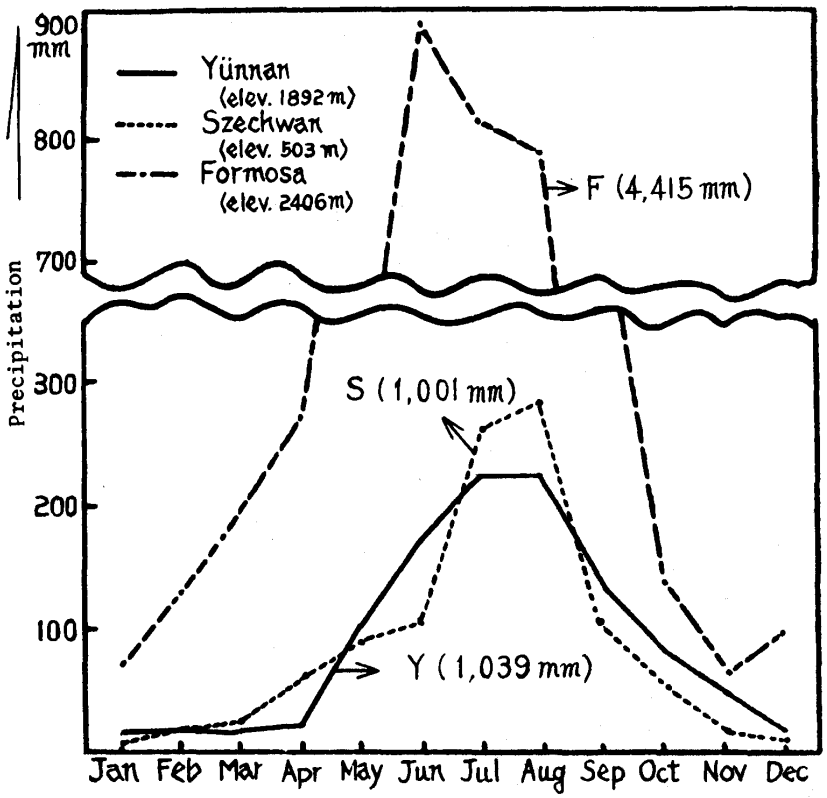


Figure 21. Distribution of precipitation over the range of *Pinus armandii*.

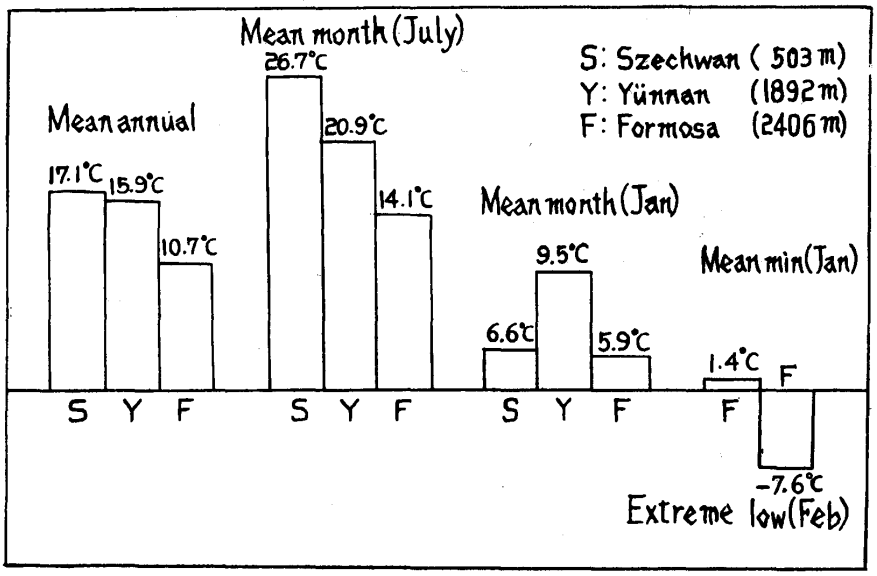


Figure 22. Range of temperature over the natural range of *Pinus armandii*.

On Taiwan, the soils on which *P. armandii* is thriving are derived from tertiary shale and slate. Armand pine is found commonly on mountain stony soils with fair growth, but it shows best growth on mountain humus soil. However, it also occurs on Yellow Earths and Red Loams, and in some locations grey-brown podsolic soils are formed under the natural forest of *P. armandii*. On both the Chinese mainland and Formosa, *P. armandii* is growing at high elevations which belong to the temperate forest zone (Jih-Ching Liao, *personal communication*).

SILVICULTURAL CHARACTERS

Armand pine is a tree up to 20 m in height, with widespreading horizontal branches and thin, smooth, greenish bark (Fig. 23). Leaves, in fives and persisting 2 to 3 years, are slender, 8 to 15 cm long, serrulate, bright green spreading or drooping, usually sharply bent near the base. Cones are cylindrical.



Figure 23. Bark of a 40-year-old *Pinus armandii* (H = 15 m, DBH = .4 m, photo by Mr. J.-C. Liao).

Germination of seed is quite easy, as is natural regeneration. However, it is recommended that the seedlings be raised in polyethylene bags by transplanting each cotyledonal seedling into the bag when they reach 5 to 6 cm in height. Seedlings should be planted on rainy days. In order to prevent frost heaving, trampling around the planting stock during the first winter after planting is needed (Liao, *personal communication*). However, artificial planting seems not to be a common practice in either the Chinese mainland or Formosa.

P. armandii is an important timber source in Formosa with a total volume in the central mountain ranges in Formosa of around 3,500,000 m^3. Reports on damage caused by pests or diseases are unknown to the author.

GROWTH PERFORMANCE

No records on the growth performance on the Chinese mainland are available. However, a report is available on the growth performance of a natural stand in the central mountain ranges of Formosa (Fig.24 and 25).

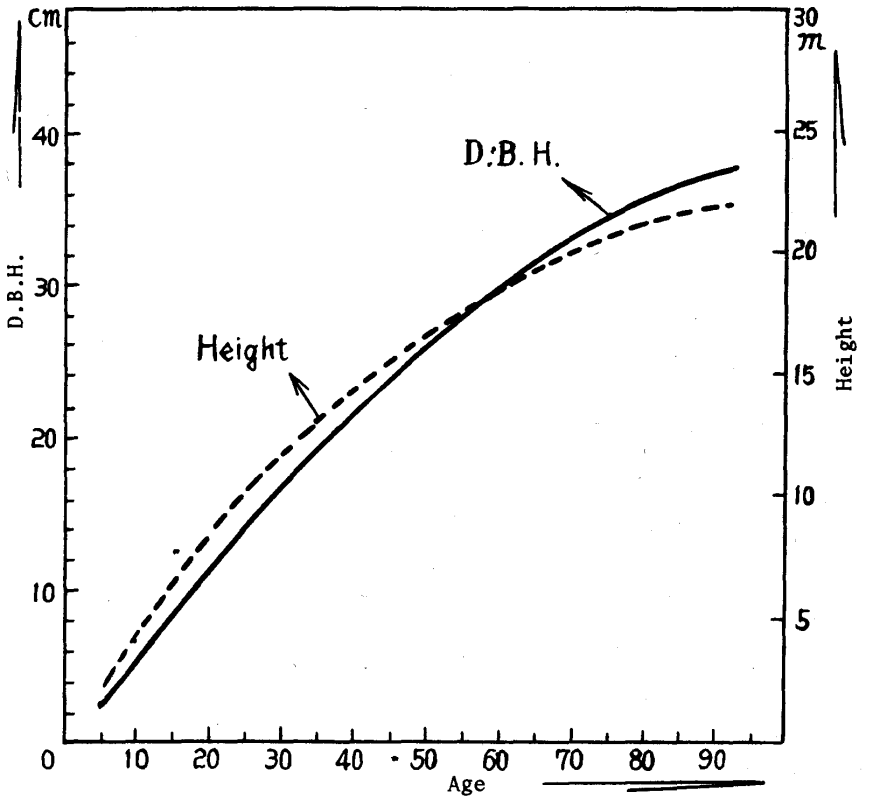


Figure 24. Height and diameter growth of an average *Pinus armandii* in a natural stand on Mt. Alishan, Taiwan. Drawn from data provided by Mr. Jih-Ching Liao, Assistant Professor of Dendrology, Taiwan University, Taipei, Taiwan.

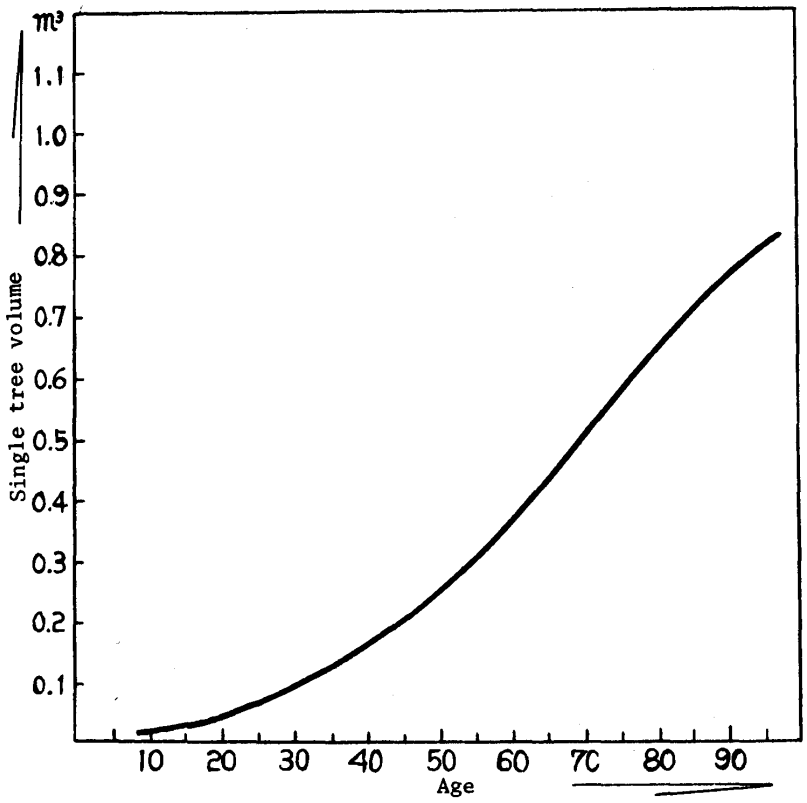


Figure 25. Volume growth of an average *Pinus armandii* in a natural stand on Mt. Alishan, Taiwan. Drawn from data provided by Mr. Jih-Ching Liao, Assistant Professor of Dendrology, Taiwan University, Taipei, Taiwan.

The growth performance under introduction is not known,but there is a report (Dallimore and Jackson, 1923) that it grows rapidly at Kew in light, well-drained loam under similar conditions to *P. excelsa* Wallich (Syn. *P. wallichiana* A.B. Jacks.). Trees 20 years old cone freely and some of the seeds are fertile. Two planted stocks of *P. armandii* at the Asakawa Experimental Forest in Tokyo, Japan, are not so healthy (Fig. 26).

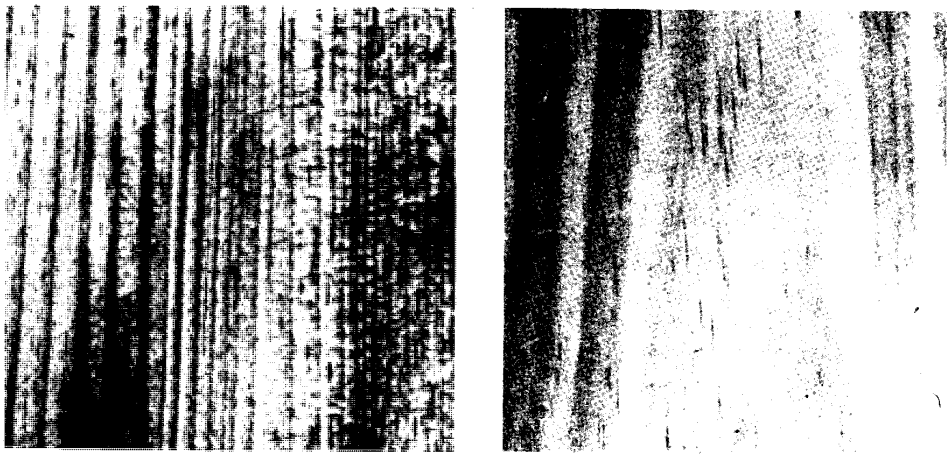
TIMBER QUALITY

P. armandii is characterized by pale, yellowish-white sapwood and yellowish-brown heartwood which is clearly distinguishable from the sapwood. It is straight-grained and medium- to fine-textured. Growth rings are distinct, wide, and uniform in width (Fig. 27). Transition from springwood to summerwood is abrupt and delineated by a broad band of darker summer wood. Wood rays are very fine and not visible to the naked eye. Under a hand lens they appear to be whitish or brownish and contain a horizontal resin duct, forming a fine, close fleck on the quarter surface.



A. B.

Figure 26. A) 9-year-old and B) 20-year-old *Pinus armandii* trees planted in the Asakawa Experimental Forest, Japan (provided by Dr. H. Saho).



A. B.

Figure 27. A) Radial section and B) tangential section of *Pinus armandii* wood.

Resin canals are present, axial and radial, and are conspicuous, but the wood has no characteristic resinous odor or taste. The average fiber length and width are 5.33 mm and 57.6 μ respectively. The cellulose content is 53.97% (α-cellulose = 40.08).

The wood of Armand pine is moderately light with a specific gravity of 0.46 (oven dry), soft and very stiff, moderately strong in bending with a bending strength of 747 kg/cm^2, weak in endwise and sidewise compressive strength (376 kg/cm^2 and 56 kg/cm^2 respectively). It is also weak in tension parallel to the grain (540 kg/cm^2) and shearing (92 kg/cm^2). With an average shrinkage of 3.21% in the radial plane, 5.32% in the tangential plane, and 9.3% in volume, the wood is easy to kiln-dry and stays in place well after seasoning. The wood is moderately easy to work with tools. In decay resistance, it is rated as intermediate to fairly durable.

The wood is used principally for construction, furniture, matches, papermaking (limited to small, round timbers), boxes and crates, turpentine and rosin.

The physical properties of Korean pine, Armand pine, and eastern white pine are compared in Table 1.

Table 1. Comparison of wood properties of three white pines

Properties	*Pinus koraiensis*[a]	*Pinus armandii*[b]	*Pinus strobus*[c]
Specific gravity (oven dry)	0.45	0.46	0.37
Shrinkage (%)			
Radial	2.3	3.2	2.3
Tangential	6.3	5.3	6.0
Volume	8.9	8.4	9.6
Bending strength (kg/cm^2)	551	747	540
Compressive strength (kg/cm^2)	321	376	280
Tensile strength (kg/cm^2)	451	540	800
Shearing strength (kg/cm^2)	62	92	55
Cellulose content (%)	54.08	53.97	59.71
(α-cellulose)	(70.68)	(40.08)	(64.61)

[a] Chosen Govt.-Gen., 1940.

[b] Chinese Forest. Assoc., 1967.

[c] Kishima, Okamoto, and Hayashi, 1962.

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FLOOR DISCUSSION

Floor discussion of this paper was withheld until the four papers on the Asiatic white pines were completed. It appears after the paper by Dr. Haruyoshi Saho.

PINUS WALLICHIANA A.B. JACKSON IN PAKISTAN

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ABSTRACT

Pinus wallichiana is one of the most important multi-purpose timber species of West Pakistan. It is extensively distributed in Southern Asia. In West Pakistan it occurs in three geographically separated areas, i.e., in the northwestern part; along the western boundary and near the southwestern extremity. Altitudinally, too, the species has a wide range of distribution. Climatically, the range of blue pine can be divided into four zones, on the basis of amount and pattern of rainfall distribution.

Considering the various ecological factors governing the distribution of blue pine, three habitats can be distinguished, viz., highly xeric habitat, xeric habitat and a mesic habitat. This indicates the plasticity and adaptability of this species.

Regarding the growth statistics of blue pine, it can be observed that it is one of the fastest growing coniferous species.

Because of the extensive range of blue pine over a variety of habitats and its discontinuous distribution, genetic variation, possibly also discontinuous, may be suspected. This contention is based upon the preliminary observations investigating the genetical variation in the natural populations of blue pine of West Pakistan and Azad Kashmir.

Blue pine is quite resistant to diseases and pests.

INTRODUCTION

Pinus wallichiana A.B. Jackson is one of the most important coniferous trees of West Pakistan. A moderately hard, pink heartwood of good quality and easy workability render it a multipurpose species. In West Pakistan it is mainly used in building construction, furniture manufacture, general carpentry, and railroad ties. It also yields an oleoresin of a better quality than that of *Pinus roxburghii* Sarg., the other important pine of this region, but is not tapped for this purpose due to the short season of resin exudation at high elevations where it occurs.

As stated by Troup (1921), "When growing vigorously and before reaching old age, this is one of the most beautiful pines of the world, its bluish drooping needles and regular growth giving it a particularly graceful appearance; as it becomes old, however, it loses its graceful form and tends to become ragged." The common English name given to this species is "blue pine" due to its blue feathery foliage. The vernacular name used for this species in Pakistan is "Kail" or "Biar".

A number of scientific names of this species have been in vogue. In addition to *P. wallichiana* A.B. Jackson, they are *P. nepalensis* De Chamb; *P. excelsa* Wall. ex Lamb; and *P. griffithii* McClelland. *P. wallichiana* A.B. Jackson in Kew Bull. 1938: 85, published in 1939, however, is the latest and is accepted by the authors; all the other names have been reported to be homonyms of certain other species (Raizada and Sahni, 1960).

DISTRIBUTION

P. wallichiana A.B. Jackson has an extensive range of distribution. It grows all along the Himalayas in an almost continuous range, extending to eastern Afghanistan, the northeastern part of West Pakistan, northern Burma, and Yunnan in China (Critchfield and Little, 1966).

In West Pakistan (Fig. 1), a geographically more or less continuous distribution occurs in the northwestern part within about 33°30'N. to 36°45' N. latitude and 71°0'E. to 75°30'E. longitude, covering Murree, Hazara, Swat, Dir, Chitral, in addition to Skardu, Gilgit, and southern part of Azad Kashmir. Besides this, the species occupies two natural distribution areas widely separated from the major part of the range; they are, (1) at the western boundary of West Pakistan (i.e., near Parachinar, Fig. 1) and (2) the species' southwestern extremity, along the Sulaiman mountain range (i.e., Takht Sulaiman, Fig. 1). Blue pine near Parachinar extends from about 33°45'N. to 34°15'N. latitude and 69°42'E to 70°48'E. longitude within Pakistan territory; it is confluent westwardly into Afghanistan. Sulaiman range forests of blue pine occur from latitude 31°30'N to 31°42'N. and longitude 69°45'E. to 70°04'E.

Altitudinal range of blue pine is from an elevation of 5,000 feet to 10,000 feet. In the Murree Hills, the pine first appears at about 4,000 feet in moist and cool northerly aspects while, on southerly aspects, it starts at about 5,500 feet. In Hazara, blue pine is well represented between 6,000 and 10,000 feet. In Chitral, Dir, Parachinar, and western part of Swat, it occurs in cool situations in the upper parts of the valleys. The pine grows in these areas due to snowfall in the winter although the summer rainfall is scanty. In the Sulaiman range, the sparse occurrences of blue pine are confined to ravines and easterly aspects. The occurrence of blue pine in this dry tract is accounted for by the presence of moisture held up in depressions or pockets in the limestone formations.

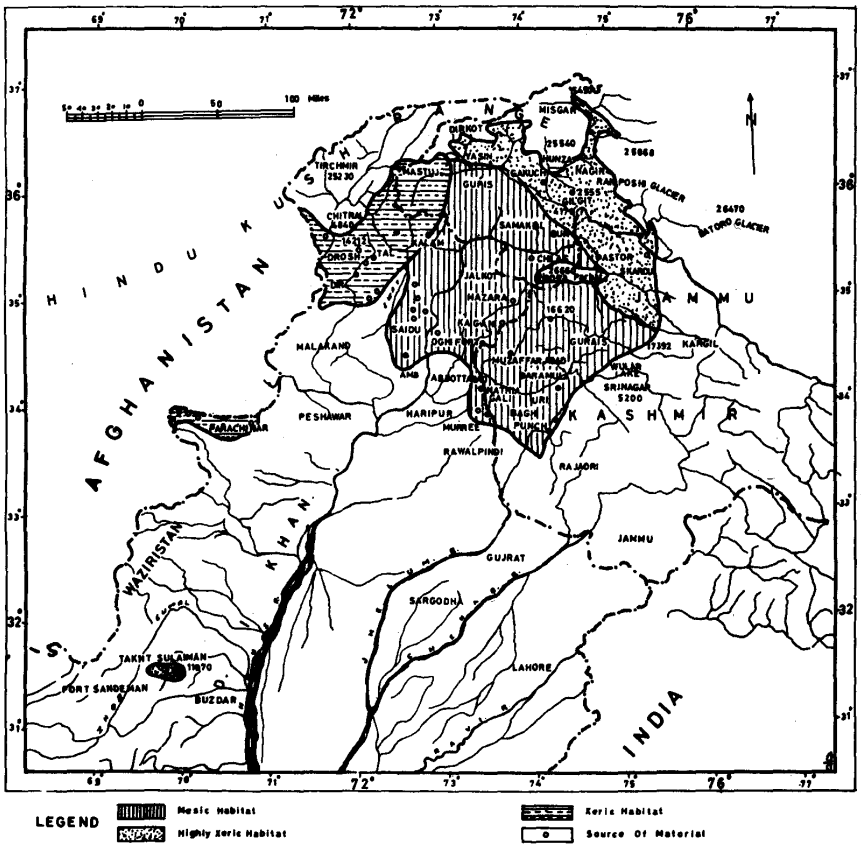


Figure 1. Distribution of *Pinus wallichiana* in West Pakistan and Kashmir.

ADAPTABILITY

As there are very few meteorological stations in Pakistan in the range of this species, observations regarding the climatic conditions necessary for its occurrence must be based upon climatological data recorded at sometimes distant stations, and upon the plant species associated with it.

Using the classification of climates as given by Ahmad and Khan (1960), the range of blue pine in West Pakistan and Azad Kashmir can be divided into 4 zones. Zone I may be called the zone of evenly distributed precipitation. Annual rainfall of this zone varies from 10 to 20 inches.

Blue pine forests of Sulaiman range are in this zone. Zone II is situated in the Himalayan rain shadow; it receives very little rain, never more than 20 inches. Thus climatically this zone is similar to Zone I, but geographically the two are well separated. Blue pine forests of Gilgit and Skardu fall in this zone. Zone III, the zone of early summer and spring precipitation, receives an annual rainfall from 20 to 40 inches. Parachinar, Dir, and northwestern part of Swat (Ushu and Atror), fall in this zone. Zone IV includes the areas with annual rainfall of 40 to 60 inches received mainly during the monsoons. Blue pine forests of Murree, Hazara, southern part of Azad Kashmir, and eastern and south-eastern part of Swat fall in this zone.

Considering the various ecological factors governing the distribution of blue pine in West Pakistan, we can distinguish three habitats.

HIGHLY XERIC HABITAT

This habitat contains areas included under climatic zones I and II, the blue pine of Sulaiman range, Gilgit, and Skardu (Fig. 2). Blue pine of Sulaiman range is associated with *Pinus gerardiana* Wall. only, whereas that of Gilgit and Skardu is mostly associated with *Picea smithiana* Boiss., *Juniperus macropoda* Boiss., and *Pinus gerardiana*. Wall. Regarding the ground vegetation the main species in the Sulaiman range are *Cotoneaster vacemiflora* (Desf.) K.Koch, *Spiraea brahuica* Boiss., *Lonicera hypoleuca* (Decne.) Jacq., *Caragana ambigua* Stock, *Ephedra* spp., *Thymus serpyllum* L., *Plectranthus rugosus* Wall., *Dichanthium annulatum* (Forsk.) Stapf., *Viburnum cotonifolium* D.Don, *Wulfenia amharstiana* Wall., *Valeriana wallichii* Decne., *Jasminum pubigerum* D.Don, *Geranium wallichianum* (D.Don) Mt. Ilam, *Buddleia paniculata* Wall., *Rubia cordifolia* L.s.l., etc. The geological formation generally consists of an intermixture of limestone, sandstone, shale, and conglomerate. Soils in this habitat are always alkaline (pH 7 to pH 8). Texturally, they are coarse (Gilgit and Skardu) to intermediate (Sulaiman range) in character.

XERIC HABITAT

Areas of climatic zone III--Parachinar, Dir, Chitral and northwestern part of Swat (Fig. 3)--comprise the xeric habitat. The main forest tree associates of blue pine in this habitat are *Picea smithiana* Boiss. *Cedrus deodara* (Roxb.) G.Don, *Juniperus macropoda* Boiss., *Quercus dilatata* Lindl., and *Quercus ilex* L. *Pinus gerardiana* Wall. occurs in drier parts and *Abies pindrow* (Royle) Spach in moister parts. Undergrowth consists of *Berberis* spp., *Viburnum* spp., *Parrotiopsis jacquemontiana* (Decne.) Rehd., *Daphne oleoides* Schreb., *Sarcococca saligna* (Don) Muell., *Skimmia laureola* Sieb. & Zucc., *Paeonia emodi* Wall., *Buxus sempervirens* L., etc. Parent rock generally consists of granite, gneiss, schist, slate, conglomerate, and dolomite formations. Forest soils in this habitat are variable, fine intermediate as well as coarse in texture, alkaline, neutral, and acidic in reaction (pH 5.4 to 7.9).



A. B.

Figure 2. *Pinus wallichiana* growing in highly xeric habitats; A. on limestone cliffs in the Sulaiman Range of climatic zone I, B. in the Himalayan rain shadow in Gilgit of climatic zone II.

MESIC HABITAT

The mesic habitat constitutes the largest proportion of the blue pine range in West Pakistan. It contains all of the areas of climatic zone IV including Murree, Hazara, southern part of Azad Kashmir, and eastern part of Swat (Fig. 4). The blue pine in this habitat is associated with *Abies pindrow* (Royle) Spach, *Cedrus deodara* (Roxb.) G.Don, *Juglans regia* L., *Picea smithiana* Boiss., *Aesculus indica* Colebr., *Quercus dilatata* Lindl., and *Quercus incana* Roxb. At low altitudes, *Pinus roxburghii* Sarg. appears while at higher altitudes *Taxus baccata* L. may also occur. *Lauracea* spp., *Litsaea* spp., and *Machilus* spp. are found locally in the moister forests. Evergreen *Euonymus* and *Ilex* are commonly associated with oak. Other common genera of the undergrowth are *Indigofera, Lonicera, Rosa, Desmodium, Viburnum, Strobilanthes, Impatiens, Senecio, Dipsacus,* and *Heracleum*. Soils in this habitat have generally been derived from slate, shale, quartz, and sandstone formations. They are intermediate to coarse textured and are generally acidic with a pH ranging from 5.4 to 6.4.

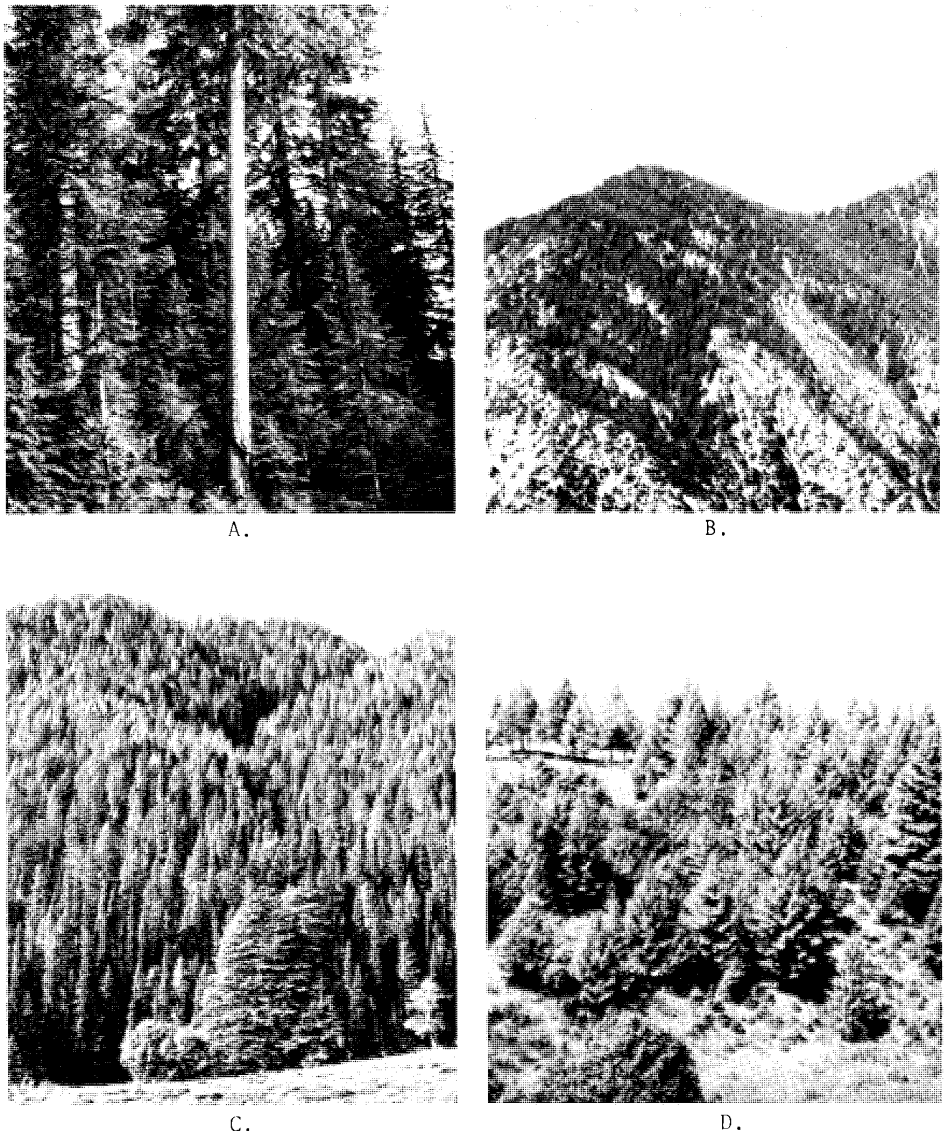


Figure 3. *Pinus wallichiana* growing in xeric habitats; A. with *Cedrus deodara* and *Abies pindrow* in Dir, B. with *C. deodara* in Chitral, C. with *A. pindrow* and *Picea smithiana* in northwest Swat, and D. in Parachinar.

The above description indicates a clear distinction in the three types of blue pine habitats. It is also quite evident that blue pine in West Pakistan is very plastic and is adaptable to extreme habitats.

The forests of Parachinar, with intermediate soil characteristics, intermediate climatic conditions, and variable vegetation, although geographically isolated from other zones, form a connecting link between the blue pine of Sulaiman range and that of Chitral, Dir, and Swat. It can be hypothesized that the two isolated southwestern populations of blue pine were once confluent. In the course of time, drying up of the



A. B.

Figure 4. *Pinus wallichiana* growing in mesic habitats; A. in Kagan, B. in southeastern Swat.

intervening areas, indiscriminate cutting, excessive grazing, and fires all have led to the existing isolated patches of blue pine. They are restricted mainly to the remote areas in the Sulaiman range, Parachinar, Dir, and Swat.

GROWTH

There are no reliable statistics available on growth and yield of this species in West Pakistan. Field data are being collected and techniques devised to prepare yield tables. These will be based on data from remeasurements of permanent sample plots as well as on single recordings from temporary plots. Growth has been found to be optimal between 6,500 and 8,500 feet elevation.

Early work on the collection of growth statistics related only to parts of blue pine range included in the mesic habitat (Hazara and Murree). A. V. Monro in 1908 and M.R.K. Jerram in 1915 (cf. Troup, 1921) measured 109 trees and determined mean diameters as given below:

Age (years)	Hazara		Murree	
	Mean diameter (inches)	Ten-year diameter growth (inches)[1]	Mean diameter (inches)	Ten-year diameter growth (inches)[1]
20	7.3	3.5	--	--
30	10.8	3.5	--	--
40	14.3	3.2	--	--
50	17.5	3.2	--	--
60	20.7	3.2	13.4	4.1
70	23.9	3.1	17.5	3.5
80	27.0	3.2	21.0	3.5
90	30.2	3.2	24.5	2.9
100	33.4	2.9	27.4	2.2
110	36.3	2.5	29.6	2.2
120	38.8	--	31.8	--

[1] *For following 10-year period.*

Although the sample taken by these British foresters represented only a fraction of the entire range and was too small to yield much reliable information, it does indicate the rapid early growth of *P. wallichiana* and the continuation of a good growth rate through age 80 to 100 years.

Using graphic methods, yield tables of blue pine were compiled by Champion, Suri, and Mahendru (1929). These tables give a fairly good idea of growth and yield of this species in the Murree area, but perhaps have little application to other parts of blue pine range. Three quality classes were recognized, as given below:

Site quality (class)	Age (years)	Mean height (feet)	No. of plots
I	90	120-140	7
II	90	100-120	14
III	90	80-100	3

From this information it can be inferred that the quality of stands of this species in areas of the mesic habitat is mostly I and II of Champion's classification.

According to Champion's yield tables, the mean annual increment of 235 and 178 cubic feet per acre is maximum at ages 80 and 100 for quality class I and quality class II, respectively. The total yield including that from intermediate thinnings is estimated to be 18,000 cubic feet per acre at the age of 90 years. Thus the species is very fast growing (Fig. 5). The trees selected in a seed production area in Kagan (Hazara), when compared with the general stands of blue pine in height and diamter, show that given favorable environment the species has a great potential for fast growth.

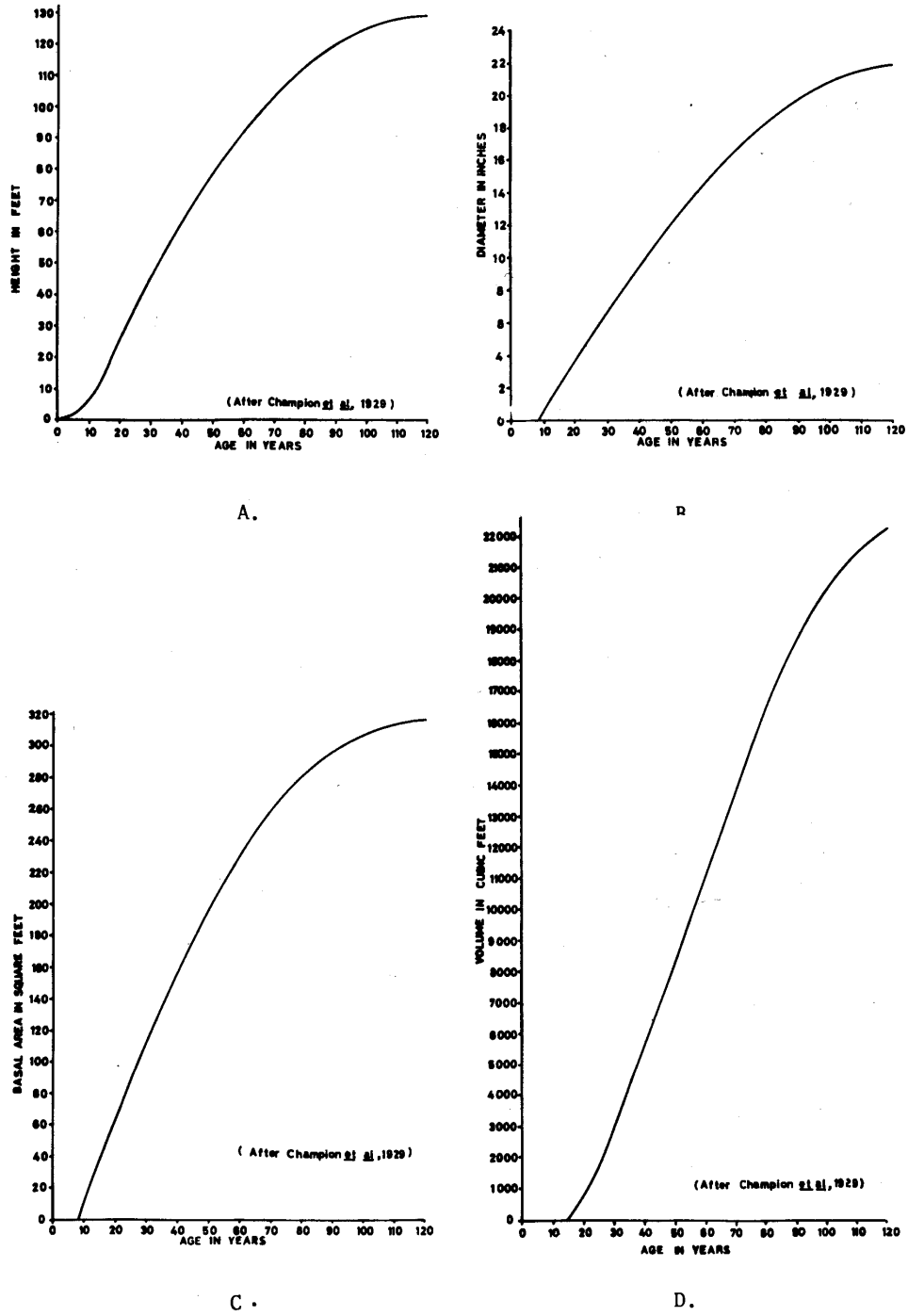


Figure 5. Growth curves for *Pinus wallichiana* on site quality I and II, in the Murree area of the mesic zone; A. height-age, B. diameter-age, C. basal area-age, and D. volume per acre-age.

GENETIC VARIATION

Because of the extensive and discontinuous range of blue pine over a variety of habitats, discontinuous genetic variation may exist.

A project to investigate genetic variation in blue pine was started in 1967 at the Pakistan Forest Institute, Peshawar. Material consisting of twigs, cones, and seed is being collected from localities throughout the range of blue pine in West Pakistan (Fig. 1). The material is collected from 10 trees representative of the stand in each locality. Morphological and anatomical studies on the cones and needles are underway. Differences among characters of blue pines of the various habitats only can be surmised at present. Definite results will be available only after the study is completed. The interim results indicate that the blue pine seed from the highly xeric habitat is small and reddish brown in color, whereas that from the mesic habitat is large and greyish to black. The following preliminary observations show quite pronounced differences in the seed size from various localities.

	Mesic habitat		Xeric and highly xeric habitats				
	Murree	South-west Swat	North-west Swat	Dir	Sulaiman range	Parachinar	Gilgit
Average seed length (cm)	0.84	0.84	0.80	0.81	0.74	0.77	0.67
Average seed breadth (cm)	0.50	0.52	0.49	0.50	0.47	0.48	0.45
Average No. of seeds per pound	6,960	6,430	7,425	6,210	9,360	8,000	10,080

Observations recorded for needle length of the few localities covered so far again indicate that drier localities (Parachinar, Gilgit, Sulaiman range, Dir) have shorter needles and the moister localities have longer needles.

	South-east Swat (Beha)	Parachinar (Speena shaga)	Gilgit	Sulaiman range	Dir (Patrak)	North-west Swat (Atror)
Average needle length (cm)	14	11	12.2	12.5	13	13.3

SUSCEPTIBILITY TO PHYSICAL AND BIOLOGICAL INJURIES

Blue pine suffers from snow more than any other conifer of West Pakistan. The snow clings to the crown, either causing top breakage or

uprooting the whole tree. The species is also very sensitive to fire, even large trees often succumbing.

Among fungus pests of blue pine, *Fomes pini* (Thore) Lloyd is the most important. This pathogen has been found most commonly in forests of the mesic habitat (Khan, 1960). Its attack results in the rotting and disintegration of the heart wood. Sporophores appear on the stems or on exposed roots at points where some injury has occurred. According to Troup (1921), lopping of branches for fodder and fuel is the most important cause of the spread of the disease.

Cronartium ribicola J.C. Fisch. ex Rabenh. is a severe stem rust of blue pine. Mostly it attacks seedlings and saplings from 3 to 10 years of age. Fortunately, it is found only rarely, and hence is of little economic importance. Ahmad (1956) collected it from Shogran in the Hazara district of West Pakistan.

A number of other fungus disease which occur rarely on blue pine of West Pakistan have been listed by Khan (1960):

1. *Lophodermium pini-excelsae* Ahmad, causes needle cast in moist and shady localities.

2. *Dasyscypha fusco-sanguinea* Rehm.emend. Hoenzel, sporadically kills young plants of blue pine in Kagan valley of the Hazara district.

3. *Cenangium ferruginosum* Fries, kills young blue pine plants about 10 years old, in moist localities.

4. *Fomes annosus* (Fr.) Cke., confined to moist localities only, causes a serious root rot once established in conifers.

5. *Fomes pinicola* (Swartz) Cke., occurs mainly on dead wood, but as a wound parasite, it has been seen on weakened living trees in Murree, Hazara, and Azad Kashmir.

Blue pine in West Pakistan is also liable to be attacked by a large number of insect pests. Again the attack is never widespread or severe enough to cause alarm. The beetles and larvae of *Hylobius angustus* Faust damage samplings. The larvae of the moths *Dioryctria abietella* Schiff and *Euzophora cedrella* Hampson bore in green cones.

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FLOOR DISCUSSION

Moderator Bingham withheld discussion on this paper so that it might be discussed with all four papers on the Asiatic white pines. Discussion follows the paper by Dr. Haruyoshi Saho.

INTRINSIC QUALITIES, GROWTH- AND ADAPTATION-POTENTIAL OF *PINUS WALLICHIANA*

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Blue pine (*Pinus wallichiana*, syn. *P. griffithii*) in the Himalayas has a wide adaptation. Seven altitudinal provenance types are recognized. Four are adapted to the outer moist and inner dry northwest Himalayas; and three, to the outer wet, middle moist and inner dry eastern Himalayas. The major blue pine forests grow in Kashmir, Himachal Pradesh, Uttar Pradesh and Nepal. In these regions the best growth is that of the moist upper level blue pine and the dry low level blue pine. Bhutan is the major blue pine area of the east. High fertility, abundant seed production and adaptation of the species to various regions are responsible for its wide distribution. A weak reproductive barrier exists between the blue pine populations growing at lower and higher altitudes of both moist and dry zones but a strong reproductive barrier is functional between the moist and the dry arid zone blue pine populations in Himachal Pradesh and Uttar Pradesh. Genotypical differences can, therefore, be expected to be present in these provenance types.

INTRODUCTION

Pinus wallichiana A. B. Jacks. (syn. *P. griffithii* McClell.), the blue pine, belonging to the soft and white pine group *Strobi*, section *Haploxylon* (Shaw, 1914, 1924), and *P. roxburghii* Sarg. are the two commercially important and widely distributed pine species in India.

Blue pine is highly resistant to blister rust caused by *Cronartium ribicola* J.C. Fisch. ex Rabenh. *P. wallichiana* crosses with the other white pines have produced hybrids resistant to blister rust which show adaptability, good growth, and hybrid vigor (Wright, 1953, 1959, 1962; Righter and Duffield, 1951; Duffield and Righter, 1953; Heimburger, 1958, 1961; Bingham, 1967). The good seed-set seen in some of the interspecific cross-combinations with *P. wallichiana* makes large-scale production of hybrids possible.

The germ plasm of *P. wallichiana* used in crosses with other white pine species is probably of unknown geographic origin. Performance of the hybrids is, therefore, based on qualities of a few biotypes at the most. Naturally, these provide only a preliminary estimate

of the genetical potential of the species. Information on the different provenances of *P. wallichiana* growing in the Himalayas should, therefore, be useful to tree breeders in planning provenance tests and breeding programs.

DISTRIBUTION

The blue pine occurs within latitudes 25°N to 36°N and longitudes 68°E to 100°E along almost the entire length of the Himalayas (Fig. 1). Its altitudinal range, from 4,000 to 12,500 feet or even more, is greater than that of any other Himalayan conifer.

In the northwest Himalayas, the blue pine grows in abundance in the Kashmir, Himachal Pradesh, and Uttar Pradesh. It is absent from some regions of Kumaon but reappears in Nepal. In the east, natural forests of blue pine are absent in Sikkim but are found in the Chumbi Valley on the Tibetan side of the Sikkim border. The species is again abundant in Bhutan but further eastward it is found only in small scattered patches in Assam and on the north and east of the Brahmaputra.

In horizontal distribution, the blue pine of the dry extreme northwest is separated from that of the wet eastern regions by over a thousand miles. Provenances from these two distinct climatic zones, therefore, differ in their silvicultural requirements (Tables 1, 2). Information is available on the blue pine of the northwestern and Nepal Himalayas (Troup, 1921; Osmaston, 1922; Champion, 1936; Schweinfurth, 1957; Nakao, 1955; Kawakita, 1956), but little is known of blue pine forests of the eastern parts (Troup, 1921; Schweinfurth, 1957; Champion, 1936; Shebbeare, 1934; Ward, 1942).

The blue pine shows two distinct zones in the Himalayas, (1) the moist southern outer zone, and (2) the dry northern inner zone beyond the reach of monsoon rainfall (Fig. 6, Tables 1,2).

The following account of its provenances is based on my personal observations in the field from 1954 to 1965 on the blue pine distributed vertically from 4,000 to 12,000 feet, from Beas to Ganga Valley, and breadth-wise from Simla to Shipki pass (Sutlej valley, Fig. 6, see Dogra, 1964a) and from Mussoorie to Gangotri glacier (Bhagirathi - Ganga valley) and on observations of others (mainly Troup, 1921; Osmaston, 1922; Champion, 1936; Nakao, 1955; Kawakita, 1956; and Schweinfurth, 1957).

PROVENANCES FROM NORTHWEST AND NEPAL HIMALAYAS

The blue pine forests extend from Kashmir to Kumaon at elevations from 4,000 to 12,500 feet or over (Fig. 1). This region is the biggest blue pine area. The best forests grow between 6,000 and 9,000 feet. In Kumaon, blue pine is found only in the dry zone; in the southern moist zone, the species occurs only in few localities and is absent east of the river Pindar (Osmaston, 1922). Except for this gap, the distribution is continuous from Kumaon to Nepal (Fig. 1).

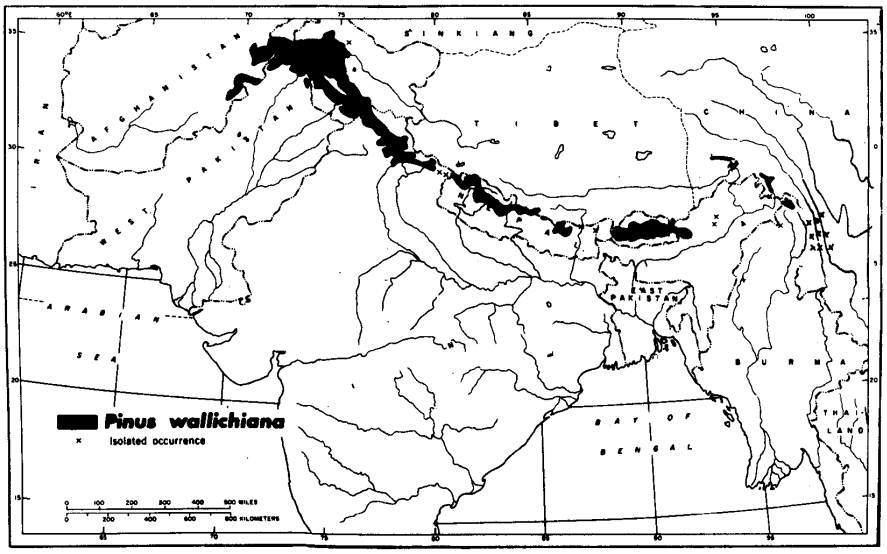


Figure 1. Map showing distribution of blue pine in Himalayas; from Critchfield and Little, 1966.

MOIST LOWER-LEVEL MONSOON ZONE BLUE PINE

The blue pine grows in limited open forests above the *Pinus roxburghii* belt. *P. wallichiana* may at places mix with the upper limit of the *P. roxburghii* belt or grow below it because of soil preference.

Habitat and Soil

These forests prefer cool, protected, well-drained, rocky mountain sites. They occur on grassy slopes, abandoned cultivated land, poor soils near low-lying villages, landslips, and forest land destroyed by fire. Mostly occurring in pure stands, they are also found mixed with broad-leaved trees and higher up with *Cedrus deodara* (Roxb.) G. Don and *Quercus* spp. In Kulu, blue pine grows mixed with or below *P. roxburghii* because of preference for soils like moist mica-schists or alluvia over quartzite (Troup, 1921; Puri, 1960). In Jalkurgad in the Ganga valley, the moist lower-level blue pine grows and spreads into *P. roxburghii* forests. In Nepal, this pine grows at a higher but narrower altitudinal range from 5,900 feet to an unknown upper limit.

Tree Growth and Description

The blue pine trees here are not tall, but show good vegetative growth and are well branched, often with light bluish glaucous-green, dense foliage of relatively longer and more flexible needles than in the moist upper-level blue pine.

Flowering, Pollination and Seed-Set

Flowering and seed-set are fairly good. In Simla hills (4,500 feet) and in Giri valley (4,000 feet) the stands flower and shed pollen during the second half of April, about 7 to 10 days earlier than the moist higher-level blue pines of Huttoo peak (10,500 feet). Female receptivity,

Table 1. Description of the blue pine provenances of northwest India and Nepal

Provenances	Location	Elevation	Seasons	Biological Aspects	Pollination period[a]
Dry or arid high level area	Non-monsoon area - north of the Himalayan Range of Kashmir, Himachal Pradesh, Uttar Pradesh and Nepal	10,000-12,500 ft.	SPRING: Almost absent. SUMMER: Very short, dry or arid with no rainfall. AUTUMN: Almost absent. WINTER: Very heavy snowfall, over 15 ft. in depth at high altitudes in dry zone; less in arid zone. Night temperatures below freezing point. Snow slides and avalanches common.	Trees short, growth slow. Foliage, dark blue-green. Forests not extensive, pure or mixed, scattered with very open patches, occupying very steep slopes at high altitudes or gentle slopes of inner arid valleys. Cones and seed not abundant. Fertility not high.	June 1-15
Dry low level area	Non-monsoon area - north of the Himalayan Range of Kashmir, Himachal Pradesh, Uttar Pradesh and Nepal	6,500-10,500 ft.	SPRING: Short, frosts. SUMMER: Short, dry, little or no rainfall, days hot, nights cold. AUTUMN: Short, frosts. WINTER: Heavy snowfall ranging 7-18 ft. in depth at different altitudes. Night temperatures below the freezing point.	Trees tall, growth good. Foliage, dark blue-green. Forests extensive, open. Cones large and many. Seed abundant. Fertility high.	May 15-30
Moist upper level area	Monsoon area - south of the Himalayan Range of Jammu, Himachal Pradesh, Uttar Pradesh and Nepal	6,500 - 10,500 ft.	SPRING: Well defined, frosts. SUMMER: Early, warm and dry. Late, cool humid with heavy rainfall. AUTUMN: Well defined with dew and frosts. WINTER: Very cold, light rain, frosts, hailstorms and heavy snow. Severe at higher altitudes.	Trees tall, growth excellent. Foliage, blue-green. Forests extensive, open and dense, pure and mixed. Cones large and many. Seed abundant. Fertility very high.	May 1-15
Moist lower level area	Monsoon area - south of the Himalayan Range of Jammu, Himachal Pradesh, Uttar Pradesh and Nepal	4,000-6,500 ft.	SPRING: Well defined, frosts. SUMMER: Early, hot and dry, Late, warm, heavy rainfall. AUTUMN: Well defined with dew and frosts. WINTER: Cold, not severe, light rain, frosts, snowfall absent or very mild.	Trees not tall, growth good. Foliage, light blue-green. Forests limited, open, on grassy slopes above *Pinus roxburghii* belt. Cone and seed production good. Fertility good.	April 15-30

[a] In Himachal Pradesh and Uttar Pradesh.

Table 2. Description of the blue pine provenances of eastern Himalayas, Sikkim, Bhutan and eastwards

Provenances	Location	Elevation	Seasons	Biological Aspects
Dry high level area	Southeast Tibet: Higher regions of distribution in Chumbi valley, upper gorges of Po-Tsangpo and Po-Yigrong, north of the Himalayan range.	9,000-11,500 ft.	SPRING: Frosts. SUMMER: Cool and comparatively dry. AUTUMN: Dew, frosts. WINTER: Dry, snow at upper reaches. Heavy gales. Total precipitation 40-50 inches.	Open pure crop or mixed forests with *Pinus tabulaeformis*
Moist upper level area	Upper less wet valleys in Bhutan, Assam and lower distribution in Po-Yigrong and Chumbi valleys and Northern Burma; south of the Himalayan range.	7,000-10,500 ft.	SPRING: Dew, mild frosts. SUMMER: Heavy rainfall, 60-70 inches. warm and moist, mists, dew. AUTUMN: Dew, frosts. WINTER: Heavy frosts, some snow, wind-gales frequent.	Open or dense pure or mixed forests. Growth excellent.
Wet lower level area	Lower valleys in Bhutan, Apa Tani Aka hills, Mishmi hills in Assam, and northern Burma; south of the Himalayan range.	4,000-6,000 ft.	SPRING: Not definite. SUMMER: Very heavy rainfall, 100-200 inches. Hot, wet, mists common, windy. AUTUMN: Not definite. WINTER: Mild, heavy dew, windy.	Open forests on grassy slopes at some places with bamboos and *Podocarpus neriifolius* .

as judged from the condition of the ovular micropyles during pollination, is of very short (4 days) duration.

In Kanatal-Mussoorie hills (6,000 feet), pollination was observed on April 15, but on the same date in the same region, the moist upper level pine growing on Surkunda peak (9,000 feet) showed immature male cones with unshed pollen.

MOIST UPPER-LEVEL MONSOON ZONE BLUE PINE

The trees grow in open and dense pure crop or in mixed forests mostly with *Cedrus deodara* but also with *Abies*, *Picea*, *Taxus*, *Cupressus*, *Tsuga*, *Juniperus*, *Quercus*, *Rhododendron*, *Populus*, and other broad-leaved species. These blue pine trees show the best growth of the four altitudinal types (Figs. 2 and 4).

Habitat and Soil

The trees grow on a large variety of rocks and soils, mostly quartzites, schists, granites, alluvial and scree deposits, and limestone. Blue pine seedlings thrive on scree masses formed during monsoons from landslips mostly of mica schists with seams of phyllite, quartzite, or granite. The old screes, therefore, have excellent trees growing on them.

Blue pine does best on well-drained, moist, and deep soil, even with limestone. In very wet sites, blue pine grows only on steep slopes where gravel, rocks, and boulders are intermixed with the soil.

In the moist zone of Kumaon, blue pine is present only on limestone, but on exposed slopes with shallow soils especially of limestone, trees remain stunted.

Pure, even-aged crops of blue pine grow in the lower and upper altitudinal limits on open southern slopes of hills like Jakko (8,000 feet), Mahasu ridge (8,000 to 9,000 feet) and Mashobra (7,000 to 8,000 feet) in Simla hills. They also occur in patches on well-drained northern exposures in dense forests of oak, spruce, and fir. In these, the blue pine occupies only those parts of the forest floor which receive sufficient light through openings in the dense forest canopy.

Tree Growth and Description

The trees in general are densely branched and show good heights and girths (Jubbal and Jaunsar, Figs. 2, 3, and 4). They appear to be faster growing than the low-level pines of the dry zone (compare Jubbal and Pangi, Fig. 2). Troup (1921) estimated that blue pine in Tehri Garhwal attains a 6-foot girth after 91 years of growth, giving a mean annual girth increment of 0.79 inches. The trees are not long lived, however, and the growth rate slows down at the age of about 180 years (Figs. 2, 4, and 5). The oldest tree reported by Champion is 275 years in age (Champion and Trevor, 1938).

Good trees may measure on an average 130 to 180 feet in height and 6 to 12 feet in girth with a crown width of 30 to 35 feet. In the moist zone in Kumaon, where the blue pine is rare, height generally does not exceed 120 feet (Osmaston, 1922).

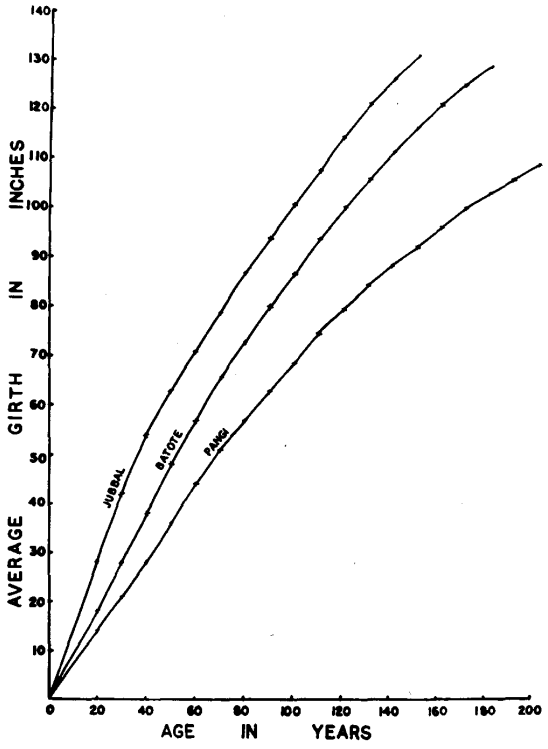


Figure 2. Average girth growth of moist upper-level monsoon zone blue pine at Jubbal (Himachal Pradesh) and Batote (Jammu) and of dry low-level non-monsoon zone blue pine at Pangi, upper Chenab valley (Himachal Pradesh).

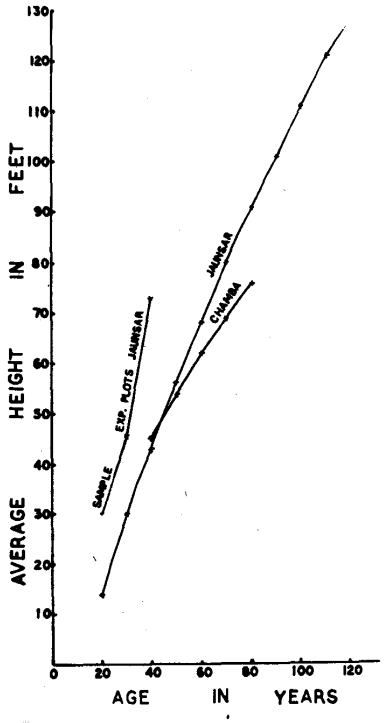


Figure 3. Average height growth of moist upper level blue pine in Jaunsar (Uttar Pradesh) and in comparatively drier region Chamba (Himachal Pradesh).

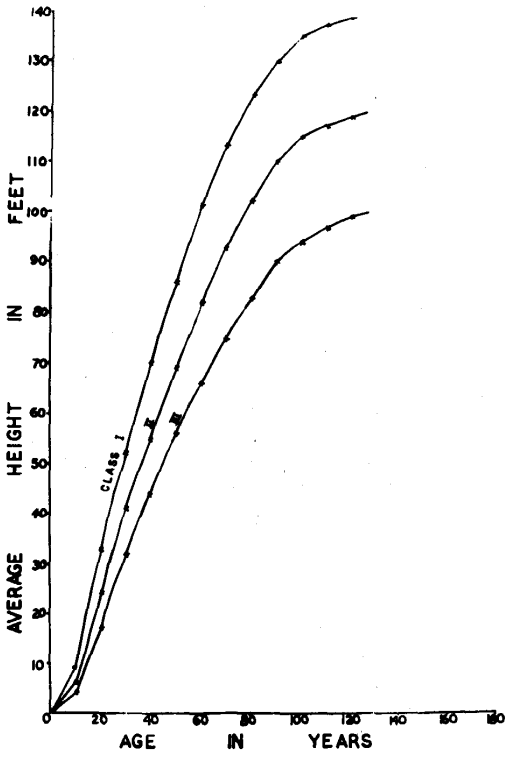


Figure 4. Average height growth of moist upper level blue pine class I (avg. ht. 120'-140'); II (avg. ht. 100'-120'); and III (avg. ht. 80'-100'), 90-year-old trees.

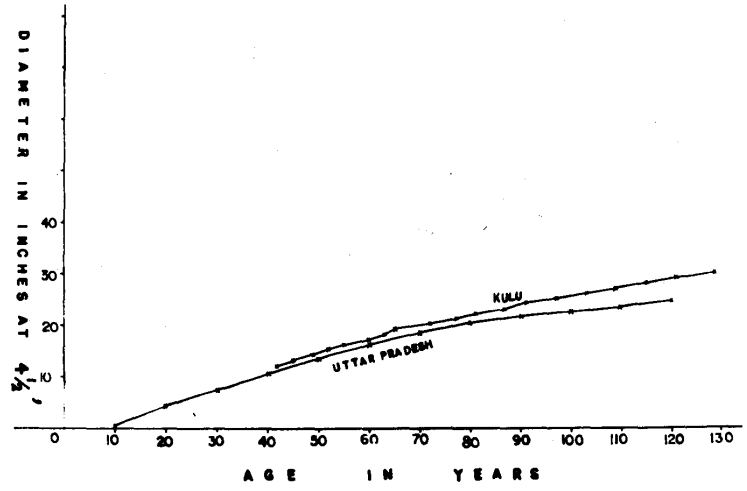


Figure 5. Average diameter growth at 4.5' level of moist upper level blue pine from Uttar Pradesh and Kulu (Himachal Pradesh). Based on measurement tables from Troup (1921) and Howard (1928).

Blue pine trees in open forests bear large spreading crowns. But in a dense, even-aged crop, the crowns may be conical or truncated. Tall, conical trees ending into leader shoots grow under open canopies of dense fir and spruce forests. Tall trees with truncated crowns were also observed growing in regions of heavy snowfall on ski-slopes of Kufri near Simla. Snow injury to the leader shoots may perhaps be responsible in giving these shapes to the trees.

Isolated trees growing on grassy slopes or on sites where forests have previously been removed usually show unbranched, lopped, or clean boles and small rounded or conical crowns. These trees are not wind-hardy and I have observed that they break down during wind storms. The crowns of these trees disperse seeds over large areas.

The few dwarf trees observed on mountain tops may be stunted due to sub-alpine effect but these trees are not typical moist upper level blue pine trees, which, in general, show good heights.

Trees growing in bright sun show excellent heights and bright blue-green and glaucous foliage. The needles are comparatively shorter and stiffer than those of trees growing in deep shade. Flowering and seed production is most abundant on these trees. The trees growing under deep shade are shorter and have loose branches, drooping foliage and flexible needles. The blue pine, therefore, is a light-demanding species.

Flowering, Pollination and Seed-Set

Most trees of the moist upper-level pine produce abundant flowers, long cones and highly fertile seeds starting at an early age. Some trees start flowering when 10 to 12 years old but 18 to 20 years is the normal age of good flowering. Flowering and pollination take place in the first half of May about 7 to 10 days later than in moist lower level pine growing at 4,000 feet elevation.

Annual production of abundant cones and highly fertile seed was observed on many trees between 1954 and 1965. Bumper seed crop years were observed at 2 to 3 year intervals. These bumper crops are more frequent in the blue pine than in any other Himalayan conifer. The amount of seeds produced during these periods is remarkable. Production of abundant seed, their efficient dispersal from the cones during November and December, protection on the ground by snow, and the high adaptability that the seedlings show to all types of soil makes possible rapid colonization of new areas by *P. wallichiana*.

DRY LOW-LEVEL NON-MONSOON ZONE BLUE PINE

The trees grown in open formations and in pure or mixed species stands mainly with *Cedrus deodara* but also with *Pinus gerardiana* Wall., *Cupressus torulosa* Don., *Abies* and *Picea* spp. These trees are the best in the dry zone.

Habitat and Soil

These blue pine forests are found on sedimentary and scree deposits of schists, granite, and alluvia and grow best on flood plain deposits of mica-schists and fine grained moist soil on steep mountain sides or in high valleys (9,000 to 10,500 feet). In Kashmir valley the trees prefer the Karewa formation of thick lacustrine deposits and in Kinnaur they

prefer mica-schists, screes, and flood plain deposits. At Gangotri they grow on flood-plain deposits and moraines. In Kumaon, blue pine forests mixed with little firs grow on gneissic sub-soils. In Nepal they grow on alluvial plains at high altitudes.

Tree Growth and Description

At Kalpa in Kinnaur-Sutlej, these trees are tall, 60 to 140 feet in height and 6 to 10 feet in girth. The trees, in general, have conical crowns ending in leader shoots but trees with spreading or truncated crowns are also found. Branches and foliage are dense. The foliage is dark bluish green, relatively short and stiff, especially on slopes exposed to bright sunshine. The rate of tree growth is good but slower than that of the moist upper-level monsoon zone blue pine (Fig. 2). An average of 9.1 rings have been calculated per inch of radius from ring-countings of 49 stumps in Kishanganga valley in Kashmir and the mean annual girth increment is stated to be about 0.7 inches (Troup, 1921). In the dry climate trees look younger and vigorous, though older in age, because the growth is slow but good. These trees are, however, highly susceptible to attacks of *Arceuthobium minutissimum* Hook. which causes considerable damage.

Flowering, Pollination and Seed-Set

Flowering is abundant and pollination occurs during the warm, dry days of the second half of May, about 7 to 10 days later than in the high-level monsoon zone pine. May is also the flowering time at Joshimath in Kumaon (Strachey, 1906). The female receptivity period is of short duration (4 days). The trees produce cones profusely and the seed-set is good. Some trees of this zone have large and heavy seeds.

DRY OR ARID HIGH-LEVEL NON-MONSOON ZONE BLUE PINE

The trees form very open forests scattered in patches at high altitudes (10,000 to 12,500 feet or more) and on gentle slopes around arid valleys situated near the northern limit of blue pine. These valleys have an annual precipitation of 10 to 30 inches, mostly in form of winter snow (Fig. 6). The blue pine grows in pure patches or mixed with *Cedrus deodara*, *Pinus gerardiana*, *Abies spectabilis* (D. Don) Spach, *Betula utilis* Don, *Rhododendron*, *Picea* and *Juniperus* spp.

Very little is known about the dry or arid high-level blue pine because it grows in regions not easily accessible to man.

Habitat and Soil

The trees prefer gentle, protected slopes capable of holding enough snow to meet the summer moisture needs. In highly arid regions the trees may grow on stream beds near water. Blue pine also grows on very steep slopes at high altitudes with more than 15 feet of snow. Snow slides and avalanches are, therefore, commonly experienced by these trees. In fact, the blue pine often occurs on narrow marginal strips along regular paths of snow slides.

In the interior valleys, the blue pine can be found in patches on snow-holding slopes and shallow ravines protected from strong winds. Blue pine trees were seen on the way to Gangotri glacier growing on moraines

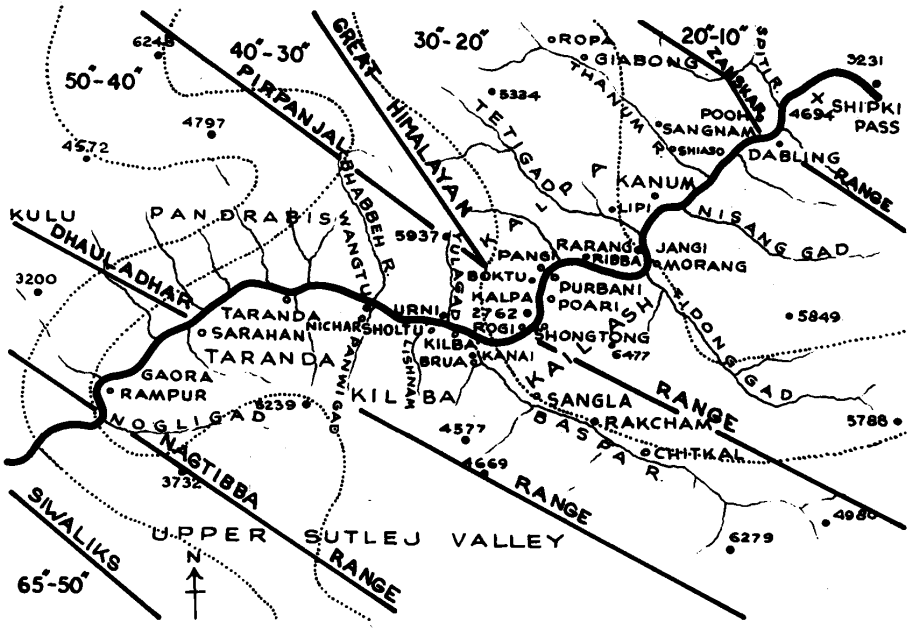


Figure 6. Upper Sutlej Valley showing outer moist zone monsoon zone separated from inner dry and arid zone by high Himalayan ranges. Point-heights in meters.

composed of clay soils and decomposing rocks and also on large boulders and coarse soil. In central Nepal the species grows on the northern flanks of Dhaulagiri and Annapurna ranges and on alluvial plains of the upper wide valleys.

Tree Growth and Description

The trees are short, 10 to 60 feet in height, and show very slow growth. Trees of small girths may be quite old. Branches and foliage are dense, often touching the ground. Needles are short, stiff, and dark bluish-green in color. The trees are drought-resistant and cold-hardy. Sliding snows, however, damage and bend the sapling stems with their weight and thus trees with curved trunks are often seen on high slopes. Avalanche winds, heavy snowfalls, and extreme aridity injure the trees and they may sometimes become ragged and gnarled. In general, however, the short dry or arid high-level blue pine tree does remarkably well in the extremely cold and arid high altitudes.

Flowering, Pollination and Seed-Set

Flowering and pollination take place in the first half of June after the snows have melted, about 7 to 10 days later than on the dry low-level blue pine. Cones are comparatively short, seed production is not abundant, and seed fertility, though fairly good, is not high. In Kinnaur, I observed

some trees at high altitudes (10,500 feet) bearing empty or half-filled seeds. Seed-radiography, embryology, and chromosomal studies of higher level blue pine may shed new light on the problem of half-filled or empty seeds in dry or arid high-level blue pine populations (Dogra, 1967).

PROVENANCES FROM EASTERN HIMALAYAS

The eastern Himalayas experience the heaviest rainfall in India. The blue pine in these regions can, therefore, be classed into three provenances: wet lower-level, very heavy monsoon zone; moist upper-level heavy monsoon zone; and dry high-level non-monsoon zone blue pine provenances (Table 2).

WET LOWER-LEVEL, VERY HEAVY MONSOON ZONE BLUE PINE

The wet lower-level, very heavy monsoon zone blue pine grows in almost tropical to sub-tropical forests of approximately 4,000 to 6,000 feet altitude which experience an annual rainfall of 100 to 200 inches.

These provenances are found in some regions of Assam. In Apa Tani valley of Aka hills, blue pine experiences an annual rainfall of 200 inches (Bor, 1938) as compared with 10 to 30 inches for blue pine of upper Sutlej valley in the northwest. It grows in open forests on exposed grassy slopes with bamboos and ferns. In Mishmi hills, it grows with *Podocarpus neriifolius* and bamboos (*Arundinaria* and *Phyllostachys*) on exposed grassy slopes at approximately 4,920 feet altitude. Blue pine has been reported to occur between the altitudes of 4,920 and 6,884 feet on grassy slopes of Ngawchang, Taron, and Seinghku valleys in upper Irrawady of northern Burma (Ward, 1944; Schweinfurth, 1957; Bor, 1953). In Bhutan the low-level pine may be found at about 4,920 to 6,840 feet with an annual rainfall of over 100 inches. The blue pine of these regions therefore seems to be well adapted to conditions of heavy summer rainfall.

MOIST UPPER-LEVEL HEAVY MONSOON ZONE BLUE PINE

Blue pine grows in the inner and comparatively drier valleys of Bhutan and Assam in pure crop or mixed with *Quercus*, *Juglans*, *Rhododendron*, *Cedrela*, *Larix*, *Taxus*, *Tsuga*, and *Picea* spp. Wallich (1832) mentions blue pine growing in Bhutan to be larger in size than that of Nepal. Some of these forests in Bhutan grow near the border regions of Bengal and Assam from 8,500 to 10,500 feet altitude but they may descend to 7,000 feet. They form a belt from valleys of Amo to Manas in Bhutan and extend slightly into West Assam. These areas show the best blue pine growth in Eastern Himalayas (Fig. 1).

The moist higher-level heavy monsoon zone blue pine also appears to grow from about 6,000 feet upwards in gorges of middle Po Tsangpo and Po Yigrong which join Brahmaputra from the north and in the higher reaches of its distribution in upper Irrawady region in Northern Burma (Ward, 1942, 1944; Schweinfurth, 1957).

DRY HIGH-LEVEL NON-MONSOON ZONE BLUE PINE

These forests are situated at 9,000 to 11,500 feet altitude mainly in the southeastern regions of Tibet behind the main Himalayan ranges in narrow valleys or gorges, e.g., the Chumbi, Po Tsangpo, and Po Yigrong valleys. In Po Yigrong, moist high-level heavy monsoon zone blue pine is found up to Temo Chamma. Further up, dry high-level blue pine occurs in mixed pine forests with *Pinus tabulaeformis*, *Populus*, *Salix*, *Quercus*, *Larix*, and *Picea* spp. or in open pure crop with *Quercus ilex* L. (Schweinfurth, 1957; Ward, 1942).

CONCLUSION

The blue pine has seven different provenances, four in the west and three in the east. In the west, the moist lower-level and the moist upper-level monsoon zone provenances form the largest forests which spread out over an extensive region of the middle Himalayas in Himachal Pradesh and Uttar Pradesh. In Kammu and Nepal, the middle Himalayan region is not so extensive and the monsoon zone blue pine grows only in a narrow altitudinal range. Therefore, the distinction between the moist lower-level and the moist-upper level blue pine types in Jammu and Nepal is not as clear as in the middle Himalayas of Himachal Pradesh and Uttar Pradesh. The moist upper-level monsoon zone blue pine forests show the best growth in these two states (Figs. 2, 3, and 4). The dry or the arid non-monsoon zone provenances, on the other hand, grow more extensively in Kashmir and in dry inner valleys of Himachal Pradesh, Uttar Pradesh, and Nepal. In Kumaon the major blue pine forests are in the dry zone. The dry low-level blue pine forests are the second best in showing good growth in India (Fig. 2). Thus Kashmir, Himachal Pradesh, Uttar Pradesh and Nepal are the major blue pine growing regions in the west (Fig. 1).

Not much is known about the three provenances of the Eastern Himalayas except that Bhutan is the major blue pine area of the east and it has excellent forests of moist upper-level heavy monsoon zone blue pine (Fig. 1).

ACCLIMATIZATION POTENTIAL

Blue pine shows a high acclimatization potential and is adapted to grow both in the extreme wet and warm low regions and arid and cold high altitudes in the Himalayas. Its absence from some areas like Sikkim and the moist zone of Kumaon is hard to explain, but cultivated trees which show good flowering and seed-set have been observed in Kumaon, Darjeeling, Kalimpong, Lachung valley in Sikkim, and Shillong (Hooker, 1855; Troup, 1921; Biswas, 1940; R. V. Sitholey, *personal communication*). R. C. Joshi has given me the following figures of growth rate from a blue pine plantation (8,000 feet) near Nainital, Kumaon.

Age	Average height (ft)	Average diameter (in)
30 years	15.8	20.8
34 years	-	22.1
39 years	18.6	25.1
46 years	-	25.3

The good growth rate and the good cone and seed production (Troup, 1921) in planted blue pine stands shows that the species adapts well to the Kumaon region.

SILVICULTURAL CHARACTERISTICS

Blue pine is a light demander. It grows and flowers best in open situations exposed to bright sunshine; it tolerates different degrees of shade but not deep shade.

It grows well both in moist and dry climate but winter snow is necessary for good growth. In dry climate, low-level blue pine is susceptible to attacks of *Arceuthobium minutissimum*.

Trees are not long-lived but begin to flower and set seed at an early age. Mature trees seed well every year and abundantly after short intervals. The seedlings are drought-resistant and well adapted to grow on a variety of soils.

The species is highly drought and cold resistant, frost and snow hardy, and can tolerate a combination of extreme cold and aridity.

Blue pine is an efficient colonizer of open grass lands, landslips, moraines, and flood plain deposits. It grows best on well-drained moist and deep soil, mostly alluvia, flood deposits, and decomposed mica-schists with gravel rocks and boulders.

Good seed-set and high fertility from an early age, coupled with efficient seed dispersal and high adaptability to a variety of soils, climates, and altitudes seem to be highly advantageous to the species in acquiring a wide distribution ranging from favorable to adverse climates.

REPRODUCTIVE BARRIER BETWEEN THE PROVENANCES

Pollination in the blue pine forests takes place during the warm and dry sunny weather of the spring. The male cones during this period enlarge, become yellow in color, and shed their pollen. Pollen is received by the fully receptive and turgid micropylar flaps of the ovules situated at the base of the scales. The micropyles are exposed to the wind in spring by the opening of the scales due to sudden elongation of the central axis of the female cone. The different periods of pollination in the blue pine populations are geared to the spring and climatic conditions of their provenances.

In Himachal Pradesh and Uttar Pradesh pollination in the moist lower-level blue pine (4,000 feet) occurs about 7 to 10 days earlier than in the moist upper-level blue pine (10,000 feet). Female receptivity in the moist lower-level blue pine is of very short duration (4 days) after which most of the micropyles shrivel up (Dogra, 1964b) and direct cross-pollination with the moist upper-level blue pine becomes difficult. Intermediate condition in regard to pollination and female receptivity periods exists in different trees growing in the middle altitudes and the gene exchange between lower- and upper-level populations in the moist monsoon zone takes place mostly through these intermediate tree forms. The same condition exists in the low- and high-level blue pine populations of dry and arid zones.

The differences in pollination and female receptivity between the moist lower-level provenance of the outer monsoon zone and the dry or arid high-level provenance of the interior non-monsoon zone is too great to allow cross-pollination between them. The reproductive barrier between the two is further strengthened by the presence of high Himalayan ranges which isolate them and exchange of pollen or seed between the two regions is not possible except through the few bottlenecked gorges. Thus a strongly functional reproductive barrier exists between the moist monsoon zone and dry-arid non-monsoon zone provenances and there is a weakly functional reproductive barrier between low and high altitude provenances in both the outer monsoon and the inner non-monsoon zones. Genotypical differences, therefore, can be expected to be present amongst the four provenances of Northwest Himalayas.

The above fact is supported by the results of preliminary experiments carried out on blue pine seed and seedling development in 1931, 1932, and 1933 at the Forest Research Station, Kulu. It is shown that seeds collected from higher levels are not suited for tree plantation at lower levels and vice versa. Similarly, seeds collected in the dry zones proved to be unsuitable for plantation in moist zone and vice versa (Suri and Seth, 1959).

An assessment of genotypical differences between the different blue pine provenances of Himalayas can be made only by replicated provenance tests and by detailed studies on the differences in rate of growth, disease resistance, morphology, periods of pollination and female receptivity, breeding system, embryo-endosperm and seed development, and in seed variation both from the field and from provenance plots.

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FLOOR DISCUSSION

Dr. Dogra was unable to attend the Advanced Study Institute. His paper was read by Dr. Howard B. Kriebel. Floor discussion was withheld until the four papers on the Asiatic white pines were completed; it appears after the paper by Dr. Haruyoshi Saho.

WHITE PINES OF JAPAN

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ABSTRACT

Five white pines native to Japan, plus several introduced white pines, are considered. Native *Pinus pentaphylla* from cool, rocky sites of northern Japan, and *P. himekomatsu* from similar, mountainous sites to the south, both exhibit slower growth but higher needle-rust and rodent-damage resistance than introduced *P. strobus*. The often dwarf and very slow-growing *P. pumila* occupies mountain-top sites throughout northern and central Japan, and is quite resistant to needle rusts. *P. koraiensis*, limited almost entirely to the central mountains of Honshu, exhibits growth slightly better than *P. pentaphylla*, but still well below that of *P. strobus*. It is highly susceptible to needle rusts. *P. strobus* is the preferred white pine introduction, but under high vole populations control of these rodents is required if it is to escape severe gnawing damage. Only limited information is now available on *P. monticola*, *P. griffithii*, *P. albicaulis*, *P. flexilis*, and *P. lambertiana*. A brief discussion of the controversy concerning the division of the species *P. parviflora* into northern (*P. pentaphylla*) and southern (*P. himekomatsu*) taxons is given. Also, some evidence for and against the presence of *Cronartium ribicola* on *Ribes* spp. and on native and introduced white pines in Japan is presented.

INTRODUCTION

Japan has a relatively rich white pine flora including 5 native species or major varieties (Fig. 1). In order of decreasing importance these are *Pinus pentaphylla* Mayr, *Pinus himekomatsu* Miyabe and Kudo, *Pinus pumila* Regel, *Pinus koraiensis* Sieb. & Zucc., and a variety (v. *amamiana* Hatusima) of *Pinus armandii* Franch. The latter variety is restricted to 2 islands south of Kyushu, and will not be considered further in this paper.

Similarly, Japan's introduced white pine flora is quite rich--and in the case of one species (*Pinus strobus* L.) of high potential value. Besides that species introductions include *Pinus albicaulis* Engelm., *Pinus flexilis* James, *Pinus griffithii* McClell. (syn. *Pinus wallichiana* A.B. Jacks.), *Pinus monticola* Dougl., and *Pinus lambertiana* Dougl. *P. strobus* has given good results in Japanese plantations, even though it suffers heavy needle-rust (*Coleosporium* spp.) infection and may be severely damaged by voles or hares.

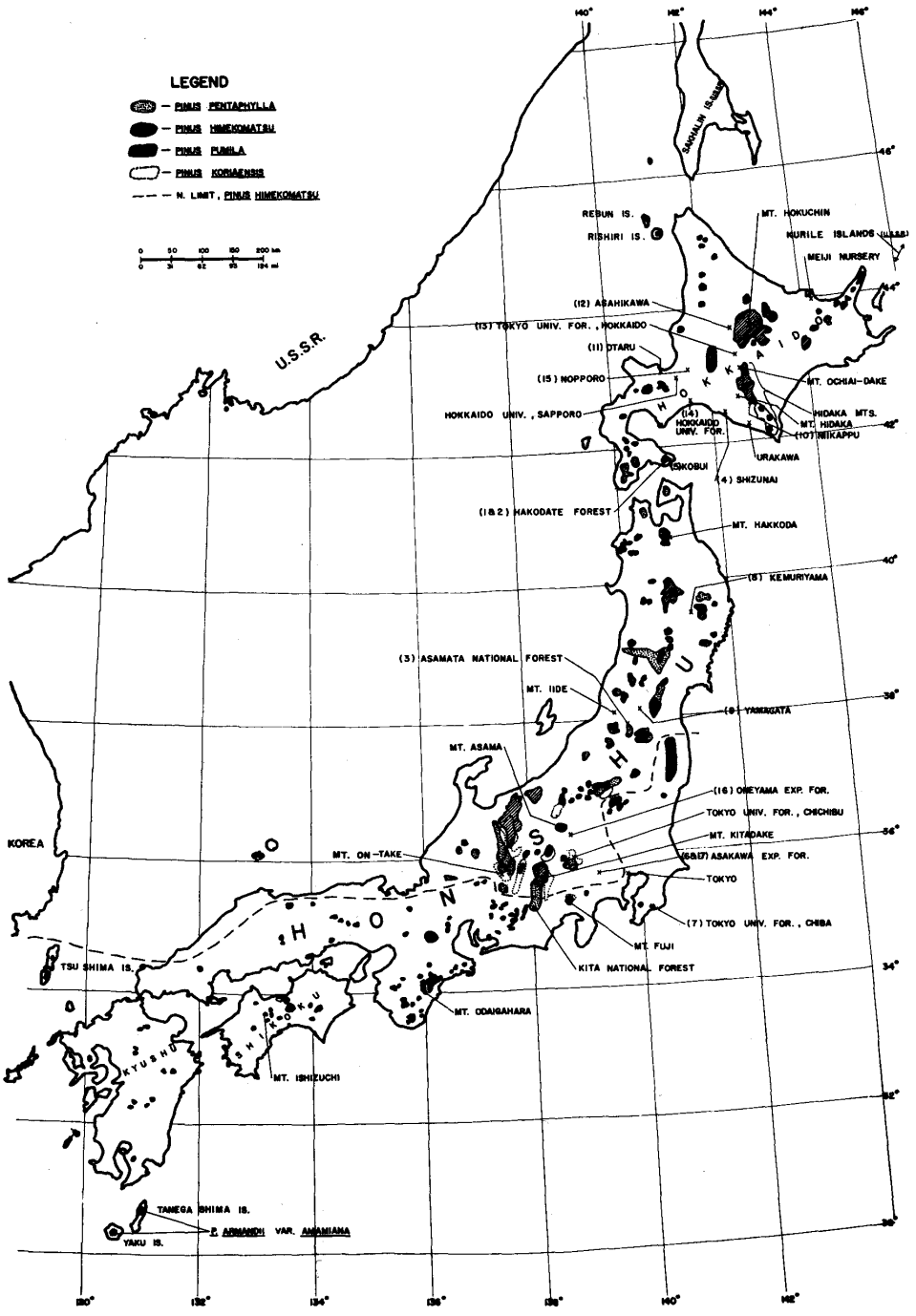


Figure 1. Approximate distribution of five native Japanese white pines (after Miyabe & Kudo, 1932, except *Pinus armandii* that is after Critchfield & Little, 1966).

TAXONOMY OF THE "*PINUS PARVIFLORA* COMPLEX"

Returning to the native Japanese white pines, the names (*P. pentaphylla* Mayr and *P. himekomatsu* Miyabe & Kudo) I have used for the first two of these are those in use by many Japanese botanists and foresters and by the pine monographer N. T. Mirov (1967). *P. pentaphylla* Mayr. is the northern taxon, and *P. himekomatsu* Miyabe & Kudo the southern taxon of the wider-ranging and morphologically diverse species *Pinus parviflora* Sieb. & Zucc. This latter single species is one often recognized outside Japan (i.e., as by Critchfield and Little, 1966).

The taxonomy of this "*P. parviflora* complex" is confused; thus controversy still exists as to which of the species names is most acceptable. Originally, Siebold and Zuccarini (1870) described the species distribution as ranging from 35°N. latitude to the Kurile Islands, and they illustrated the seeds as wingless. Later Mayr (1890) split the "complex" into 2 species describing *P. parviflora* Sieb. & Zucc. with a short-winged seed, from the south, and *P. pentaphylla* Mayr with a longer-winged seed, from the north. Still later Miyabe and Kudo (1932) reinvestigated the "complex", pointing out that Siebold and Zuccarini's original drawings of *P. parviflora* Sieb. & Zucc. (1870, Tab. 115) probably illustrated branches and foliage of the northern taxon, male and female strobili of the southern taxon, and the wingless seeds of *Pinus pumila* Regel. On the basis of these probable errors in illustration, the overextension of botanical range to the Kuriles off northeast Hokkaido (Fig. 1), and their own extensive observations on the "complex", Miyabe and Kudo rejected the single species *P. parviflora* Sieb. & Zucc. They accepted *P. pentaphylla* Mayr as a distinct and validly published species, and renamed and described Mayr's *P. parviflora* Sieb. & Zucc. (his southern species) as a new species *Pinus himekomatsu* Miyabe & Kudo.

Up to the present time, some contemporary Japanese botanists have accepted the treatment of Miyabe and Kudo (i.e., Takeda, Kusaka, and Iwate (1954), or Hayashi (1960)), while others (Makino, 1952, or Tanaka *et al.*, 1966) have relegated the southern taxon to varietal states as *P. pentaphylla* var. *himekomatsu* Makino. Undoubtedly this controversy will continue, so my choice of species names is conditional upon their stabilization.[1]

[1] *Editor's note: On October 15, 1969, the International Union of Forest Research Organizations, through its Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects, Committee on White Pine Blister Rust, recommended to the International Association for Plant Taxonomy, through their Standing Committee on Stabilization (of plant names) that the Standing Committee consider and recommend usage to stabilize these white pine latin binomials. Dr. E. L. Little, Jr., one of the United States members of the Standing Committee, has already presented the problem to the Standing Committee.*

NATIVE JAPANESE WHITE PINES

PINUS PENTAPHYLLA MAYR (NORTHERN JAPANESE TAXON OF *P. PARVIFLORA* SIEB. & ZUCC.)

The climate over the range of *P. pentaphylla* is cool. This species is distributed in areas where the annual average temperature is 7 to 14.5°C (45 to 58°F) from north to south, respectively. At the Hidaka Mountains in Hokkaido 350 to 500 m above sea level, almost at the northern limit of the natural distribution, the average minimum temperature is -14.5 to -15°C (7 to 5°F). At Urakawa, Hokkaido, this species grows near the sea coast, 50 m above sea level, on steep hills facing west. The average minimum temperature during the year is -6.9°C (about 20°F) recorded in January. At the highest place of the natural distribution on Mt. Fuji, Honshu (2500 m elevation), the average minimum temperature is about -14.7°C (6°F). Here the recorded minimum temperature was about -28°C (-18°F) observed in 1936. This is close to the -15°C average minimum observed at the Hidaka Mountains.

The southern limit of the natural distribution is at Kita National Forest, Shizuoka Prefecture, Honshu (700 to 1000 m elevation), where the average maximum temperature is 25.9 to 30.3°C (78 to 87°F). Therefore, *P. pentaphylla* can grow where average maximum summer temperatures reach about 30.0°C.

The average annual precipitation of the area of the natural distribution of this species is 1000 to 2000 mm (39 to 79 inches), in some cases 2500 to 3000 mm. Dividing the annual precipitation between summer rain and winter rain or snow discloses no relationship of summer or winter precipitation to the distribution of *P. pentaphylla*.

Soils within the range of *P. pentaphylla* are derived from andesites, shales, clay-stones, sand-stones, and tuffes. This species usually grows on the moderately moist soil, but it is rather resistant to drought and may grow in small pure stands on the ridge-top or on other fairly dry, rocky places like the slopes near the ridge-tops. When *P. pentaphylla* grows on a windy site in mixture with *P. pumila*, it assumes a windblown, snow-flattened shape quite similar to *P. pumila*.

Usually *P. pentaphylla* is considered an intolerant species but its seedlings grow better under the diffused light of the forest than do those of *Pinus densiflora* Sieb. & Zucc. *P. densiflora* usually grows in full sunlight in forest openings. When *P. pentaphylla* forests are clear-cut, no natural reproduction of the species becomes established in the resulting openings.

Extensive natural forests of the species are now limited, although scattered remnant stands remain in many places. Three samples are shown below.

(1)[2] Hakodate Forest A, Hokkaido, is located 320 m above sea level, on a 5 to 20° slope on sandy soil. It is 50 years old. The average height is 15 m, the average diameter is 18.6 cm (range 6 to 36 cm). The density is 915 trees/ha (2.5 acres), and volume is 196 m^3/ha. The annual growth is 3.9 m^3/ha.

[2] *Numbers in parentheses refer to forest and plantation locations on Figure 1 and Table 1.*

(2) Hakodate Forest B, Hokkaido, has the same topography as Forest A, and is 45 years old. The average height is 11 m, the average diameter is 18.5 cm (range 6 to 40 cm). Density is 935 trees/ha, and the volume is 226 m^3/ha. The annual growth is 6.0 m^3/ha.

(3) Asamata National Forest, Akita Prefecture, Honshu, is about 85 years old. The average height is 15 m, and the average diameter is 18 cm. Density is 1920 trees/ha, the volume is 340 m^3, and the annual growth is 4 m^3/ha. The annual precipitation of this forest is 1236 mm (48 inches), the average maximum temperature is 16.2°C (61°F), and the average minimum temperature is 6.2°C (43°F).

A remnant stand of *P. pentaphylla* is shown in Figure 2.



Figure 2. Old remnant-stand trees of *Pinus pentaphylla* growing on Mt. Hakkoda, Aomori Prefecture, in northern Honshu.

Plantations of *P. pentaphylla* occur at:

(4) Shizunai, Hokkaido; a plantation of 2 ha that was established in 1932. It is situated at 280 m above sea level on a southwest slope.

The soil is derived from serpentine covered with a layer of volcanic ash over 10 cm deep. One thousand seedlings per hectare were planted, but only 815 survive. The planting density is considered to be quite low (4000/ha or 1620/acre is common), consequently the volume is very poor being only 19 m^3 in volume. Average diameter is only 8.9 cm and average height is only 5.4 m.

(5) Kobui, Hokkaido, where the initial test plantations was established in 1933. Early growth was good, so planting was continued until 1954. The total area now planted is 118 ha. Examples of the growth in these plantations is shown below, and in Figure 3 that shows the 1941 plantation.

Planting date	Average height (m)	Average diameter at breast height (cm)
1939	8.2	13.4
1941	8.5	15.0
1942	7.8	14.1



Figure 3. *Pinus pentaphylla* planted in 1941 at Kobui in the southern part of Hokkaido.

Average density of 2670 trees/ha, volume 115 m^3/ha, and annual growth 6.46 m^3/ha. This level of growth is a little poorer than *Abies sachalinensis* Mast., the most commonly planted tree species in Hokkaido. In Honshu growth of *P. pentaphylla* is also poorer than that of *P. densiflora*. Therefore, foresters show little interest on making plantations of *P. pentaphylla*. There is another reason why *P. pentaphylla* is not planted widely. This is the heavy damage by *Gravitarmata retiferana* Wocke. Damage by this insect is so severe that few uninfested cones can be collected. Annual precipitation at Hakodate (40 km from Kobui) is 1178 mm, annual average maximum temperature 12.2°C (54°F.) and average minimum temperature 4.3°C (40°F).

P. pentaphylla is rather resistant to wood-rotting fungi, and its commonest use is for construction and home building. It is not used for pulp, because of the phenolic substances in the heart wood.

There are natural hybrids and varieties of *P. pentaphylla* as follows:

(a) *Pinus hakkodensis* Makino (1952) which is supposedly the hybrid between *P. pentaphylla* and *P. pumila*. Morphologically, it is intermediate between the two pines. The natural distribution of this dwarf pine hybrid is only in the northern part of Honshu.

(b) *Pinus pentaphylla* Mayr var. *laevis* Hara (Uehara, 1959), for which variety the differentiating characteristic is smooth-surfaced bark of both branches and trunk even when it becomes a big tree. The natural distribution is restricted to Mt. Hidaka, Hokkaido, and Mt. Iide, Yamagata Prefecture and Mt. Asama, Nagano Prefecture, Honshu. Rare trees of this variety are mixed with *P. pentaphylla* in those places.

PINUS HIMEKOMATSU MIYABE & KUDO (SOUTHERN JAPANESE TAXON OF *P. PARVIFLORA* SIEB. & ZUCC. AND SYNONYMOUS WITH *P. PENTAPHYLLA* MAYR. VAR. *HIMEKOMATSU* MAKINO)

The natural distribution of *P. himekomatsu* lies generally to the south of that of *P. pentaphylla*, mainly from 31-1/2° to 37-1/2° N. latitude. Where *P. pentaphylla* and *P. himekomatsu* grow on the same mountain slopes in the central part of Honshu the species separate altitudinally, with *P. pentaphylla* above and *P. himekomatsu* below. *P. himekomatsu* occurs along the eastern or Pacific Ocean coast in north-central Honshu, but does not occur on the Sea of Japan coast except to the south of central Honshu (see Fig. 1 and Mirov, 1967, Fig. 3-4a).

At the northern limit of the natural distribution, Fukushima Prefecture, Honshu, the average minimum temperature is about -6.9 to -7.7°C (19 to 18°F). At the highest place of its distribution, Mt. Ishizuchi (1950 m above sea level), the average minimum temperature is about -10°C (14°F). And at the southern limit of the natural distribution, Kagoshima Prefecture, Kyushu (700 to 900 m elevation), the average maximum temperature is about 28 to 30°C (82 to 86°F).

Annual precipitation is about 1000 to 3000 mm (39 to 118 inches), but at Mt. Odaigahara, the precipitation reaches about 4000 mm (almost 160 inches). This species is found in the area of heavy summer and light winter rains.

Soils within the range of *P. himekomatsu* are derived from quartzites, granites, clay-stones, sand-stones, tuffes and horn-stones. This species grows especially well on soils with granitic parent material. It is slightly drought resistant and like *P. pentaphylla* grows on ridge-tops or on steep slopes near the ridges.

Naturally regenerated seedlings of this species require more shade than seedlings of *P. densiflora*, thus regeneration cannot be expected. Utilization of this species is almost the same as for *P. pentaphylla*.

Natural stands of *P. himekomatsu* are fast disappearing. Nowadays one usually finds only remnant mature trees, as scattered individuals mixed in stands of other species, or as cultured ornamentals. Natural stands of this southern taxon of *P. parviflora* are threatened with extinction.

PINUS PUMILA REGEL

The natural distribution of this species is at the tops of mountains, except in northern Hokkaido where, as might be expected, it grows at lower elevations (less than 300 m). *P. pumila* was once considered to be a variety of *P. cembra* L. One good distinction between these two species is that the resin duct of *P. cembra* needles is in the mesophyll, while that of *P. pumila* is beneath the epidermis.

In general, *P. pumila* grows on very cold sites. In exposed and windy places, the snow-cover often is blown away and the trees are directly exposed to the cold weather; nevertheless it still grows normally for the species. It cannot survive in localities having hot summers.

The species extends to 70°N. latitude in northeastern Siberia. At the northern limit of its natural distribution in Japan (Rebun Island, off the northwest tip of Hokkaido, 45°N. latitude, at 300 m elevation), the average minimum temperature is about -11.2 to -12.5°C (13 to 11°F). At Mt. Hokuchin (2240 m elevation, the highest elevation attained by the species in Hokkaido), the average minimum temperature is about -25.6°C (-13°F). At the place of highest distribution on Honshu, Mt. Kitadake (3180 m elevation), the average minimum temperature is about -21.5°C (-4.5°F.). The southern limit of its natural distribution (35-1/2°N. latitude) occurs in Japan, where the average maximum temperature is about 18°C (64°F) at 2500 m elevation and about 25°C (77°F) at 1450 m elevation. Annual precipitation at places within the natural distribution of *P. pumila* is about 1000 to 1500 mm.

P. pumila grows on mountain ridges and in windy places where it creeps along the ground (Fig. 4); however, it grows fairly erect in the valleys and flat places where it reaches 3 to 5 m in height. Soils within the range of *P. pumila* are derived from andesites, serpentines and peridotites. This species is not found on relatively recent (Mt. Fuji) or active (Mt. Asama) volcanoes. *P. pumila* has no industrial use and no trial plantations have been established, even in high and windy places. However, its value in stabilizing water and snowsheds is often overlooked.



Figure 4. *Pinus pumila* growing near a windy ridgetop on Mt. Ochiai-dake in the central part of Hokkaido.

PINUS KORAIENSIS SIEB. & ZUCC.

The natural distribution of *P. koraiensis* in Japan is limited to the mountains of central Honshu, with one ontlier in northern Shikoku. Its northern limit is in Fukushima Prefecture (37°N. latitude), and, aside from the Shikoku outlier, its southern limit is only about 250 km away in Nagano Prefecture (35-1/2°N. latitude).

The climate over the range of *P. koraiensis* is cool. The average minimum temperature is about -11 to -13°C (12.2 to 8.6°F) in the northern part and the maximum is 27°C (80.6°F) in southern part. At the highest part of the range (2600 m elevation), the average minimum temperature is about -20°C (-4°F). Annual precipitation is about 1000 to 2000 mm. This is somewhat greater than that holding for the main distribution of the species in Korea, Manchuria, and China where the annual precipitation is about 600 to 1000 mm.

Moderately moist soils are required for *P. koraiensis*, as for *P. strobus*. Japanese *P. koraiensis* grows best under conditions of high relative humidity, and, under these conditions, the stems and branches often are covered by mosses and lichens. Soils within the Japanese range of *P. koraiensis* are derived from horn-stones, sand-stones, andesites and clay-stones. The species grows mainly on the lower slopes and on the wetter and deeper soils. Occasionally, when found in high rocky mountains, it occurs in a dwarf form.

P. koraiensis grows to 30 m in height and 1.5 m in diameter, but it does not occur in extensive, pure stands (Fig. 5). Therefore, it is difficult to calculate the total volume per hectare of this species. The average annual diameter growth is about 4 to 5 mm. This species reproduces and grows well under the moderate shade.



Figure 5. Two large specimens of *Pinus koraiensis* growing in a mixed stand on Mt. On-take in central Honshu (by the courtesy of Mr. H. Chimura).

There are several localities where plantations have been established in Japan. Notable plantations can be found at:

(6) Asakawa Experiment Forest, Tokyo, Honshu. One plantation was established in 1930, and measured in 1960. At that time, the average diameter was 14 cm (max. 22 cm) and the average height was 10 m (max. 16 m). Another plantation of 1935 origin had an average diameter of 12 cm (max. 20 cm) and height of 12 m (max. 16 m).

(7) Tokyo University Forest in Chiba, in east-central Honshu, where the plantation was established in 1930 and measured in 1960. When measured it had an average diameter of 18.3 cm and an average height of 9.0 m.

(8) Kemuriyama, Iwate Prefecture, northern Honshu, where one of the plantations that was planted in 1930 and measured in 1956 showed an

average diameter of 16.9 cm and an average height of 13.0 m. The density was 1330 trees/ha, total volume was 181.8 m^3, and annual growth is 5.55 m^3/ha.

(9) Yamagata, Yamagata Prefecture, northern Honshu, where the plantation was established in 1912 and measured several years ago (year not clearly known) when it showed an average diameter of 24.4 cm and an average height of 14.3 m. The density was 982 trees/ha, total volume was 364 m^3/ha, and annual growth was 8.68 m^3/ha.

(10) Niikappu, Hokkaido, where the plantation was established in 1930 and measured about 1960 when it had an average diameter of 14.2 cm and an average height of 8.8 m. The density was 1642 trees/ha, and total volume 134 m^3/ha and annual growth 6 m^3/ha.

(11) Otaru, Hokkaido, where the plantation was established in 1910 and measured in about 1960 when it had an average diameter of 21.1 cm and an average height of 15.7 m. Density was 1273 trees/ha, total volume 350.5 m^3/ha, and annual growth 7.3 m^3/ha.

The annual growth in these *P. koraiensis* plantations is about 2/3 that found in *P. strobus* plantations. A small but successful plantation in Hokkaido is shown in Figure 6.



Figure 6. A plantation of *Pinus koraiensis* at the Tokyo University Forest in Hokkaido. Planted in 1917.

INTRODUCED WHITE PINES IN JAPAN

PINUS STROBUS L.

In 1898, *P. strobus* was planted at Asahikawa, Hokkaido. This 70-year-old plantation is the oldest one of this species in Japan. From the outset, its growth was good and soon many foresters were impressed with the

potentiality of this species. As a result many more test plantations have been established over the years. Nowadays, *P. strobus* is the commonest foreign forest tree species planted in the northern part of Japan, especially in Hokkaido. These plantations are, presumably, free from the white pine blister rust, caused by *Cronartium ribicola* J.C. Fisch. ex Rabenh.

Among the introduced white pines, *P. strobus* has given the best results in Japanese plantations. Our foresters now have had plenty of experience in planting this species. If, over time, *P. strobus* continues to escape the white pine blister rust, this species can be planted over a much larger area in the northern half of Japan.

Performance of *P. strobus* in some of the many Japanese plantations of the species is shown in Table 1. Figure 7 shows the earliest plantation established at the Tokyo University Forest in Hokkaido in 1917, and Figure 8 a 15-year-old plantation on the same Forest.



Figure 7. A 1917 plantation of *Pinus strobus* at the Tokyo University Forest in Hokkaido, Yamabe, Furano.

Table 1. Performance of *Pinus strobus* L. in selected Japanese plantations

Plantation locality	Lat. (°N.)	Annual ppt. (mm)	Annual temp. (°C)	Annual temp. (°F)	Year estab.	Year meas.	Average diameter b.h. (cm)	Average height (m)	Tree Density (no/ha)	Wood volume (cu m/ha)	Annual volume growth
Hokkaido:											
Asahikawa (12)	43.6	1140	5.7	41							
Original planting					1898	1957	32.0	22.0	5.5	474.3	8.2
Later planting					1931	1957	14.0	8.5	3186	360.0	18.0
Tokyo Univ. Forest (13)	43.2	1200	6.0	42.8							
Earliest planting					1917	1960	27.0	18.0	--	350.0	10.0
Poor soil planting					1926	1960	22.7	14.6	791	232.0	7.0
Good soil planting					1928	1960	29.4	18.8	735	442.0	14.3
Recent planting					1960	1968	10.1	7.1	2358	82.5	6.3
Hokkaido Univ. Forest (14)	42.7	--[c]	--	--	1918	1950	18.0	11.8	2599	444.0	12.0
Nopporo[a] (15)	43.25	1185	6.7	42	1909-17	1960	31.8	19.4	539	405.0	10.1
Honshu:											
Oneyama, Gumma[b] (16)	36.4	2000	10.1	50.3	1909	1954	32.0	22.0	525	473.0	11.8
Asakawa, Tokyo (17)	35.4	1561	12.7	54.0	1943+	1965	10.0	8.6	2734	113.0	4.2
Tokyo Univ. Forest, Chiba (7)	35.2	2284	14.5	58.0							
Earliest planting					1898	1956	23.5	13.7	822	231.0	3.9
Later planting					1926	--	23.8	12.8	800	159.0	5.3

[a] After Matsui *et al.*, 1967.
[b] After Sakaguchi, 1958.
[c] No record available.



Figure 8. Another, younger plantation of *Pinus strobus* established in 1955 on the Tokyo University Forest in Hokkaido, Yamabe, Furano.

PINUS MONTICOLA DOUGL.

At the Tokyo University Forest in Hokkaido, *Pinus monticola* shows a brownish discoloration of the needles in winter to early spring. This discoloration probably results from exposure to cold winds. When *P. monticola* is planted behind windbreak trees, early growth is almost the same as that of *P. pentaphylla* (Fig. 9). Establishment of *P. monticola* forests has just started. Perhaps it will be best if any large plantations of this species are made in Honshu, rather than in Hokkaido.

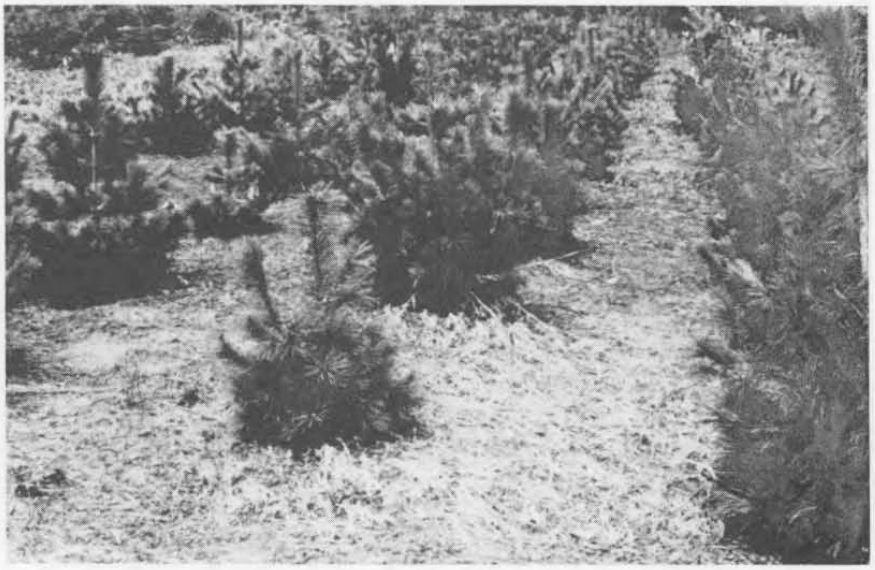


Figure 9. *Pinus monticola* from Crystal Creek, Benewah County, Idaho, 5 years after planting at the Tokyo University Forest in Hokkaido, near Yamabe, Furano.

PINUS GRIFFITHII McCLELL.

A small plot of *P. griffithii* in Hokkaido, 6 years from planting, is shown in Figure 10. Provenances of this species tested so far are very sensitive to frost damage, after which there is often an attack by *Valsa* sp. When this species is finally able to attain more than 10 m in height, as seen in Tokyo, its good growth rate begins to become apparent. *Pissodes nitidus* Roelofs attacks its shoots. Damage by this weevil is very severe on this species in Japan. As provenances of *P. griffithii* that are planted in Japan probably came from the lower slopes of the Himalaya Mountains of India, the winter weather of northern Japan may be too severe for them to show satisfactory growth.



Figure 10. Indian *Pinus griffithii* planted on the Tokyo University Forest in Hokkaido in 1964.

PINUS ALBICAULIS ENGELM., *P. FLEXILIS* JAMES AND *P. LAMBERTIANA* DOUGL.

These three species are now being tested in small stands at the Tokyo University Forest in Hokkaido. But the tops of seedlings of all species have been killed by the cold weather.

PRESENCE OF *CRONARTIUM RIBICOLA* IN JAPAN

More than 15 years ago, Professor Nobukiyo Takahashi, Director of the Tokyo University Forest in Hokkaido expressed the fear that in time *P. strobus* would be attacked by the white pine blister rust.

Already, Dr. K. Togashi had reported that in 1922 a rust believed to be *C. ribicola* was present on *Ribes latifolium* Jancz. at Rebun Island 50 miles off the northwest tip of Hokkaido (Togashi, 1924). In 1958, a cooperative group under the leadership of the late Dr. Senji Kamei of

Hokkaido University, and supported by five Hokkaido National Forests reinvestigated Dr. Togashi's alarming report. They confirmed and reported (Kamei, Igarashi, Saho, *et al.*, (1958) that the rust on *R. latifolium* on Rebun Island indeed appeared to be *C. ribicola*; more important, they also reported the rust present on *R. latifolium* at Meiji Nursery, Kitami National Forest in northwest Hokkaido.

Then, in 1959, an IUFRO Working Group concerned with internationally dangerous forest tree diseases, headed by Prof. N. Hiratsuka of Tokyo University of Education and including pathologists from the Government Forest Experiment Stations and universities, continued the search for *C. ribicola.* Again a rust, morphologically very similar to *C. ribicola*, was collected on *Ribes* in several parts of Hokkaido (Imazeki, 1963).

Finally, in 1963, a rust similar to *C. ribicola* was found on the campus of Hokkaido University on *Ribes rubrum* L., this *Ribes* species having been introduced 60 years ago into Japan. Immediately (September 16) Dr. Kamei and his Colleague Dr. T. Igarashi commenced inoculation experiments (Kamei and Igarashi, 1963), using seedlings of *P. strobus* and *P. koraiensis*. Yellow needle spots appeared on the needles of both pines, in the greenhouse 18 to 39 days after inoculation. Three years later a typical spindle-shaped, discolored stem canker with resin flow was found on the inoculated portion of one *P. koraiensis* seedling, but up to 1968 no pycnia or aecia of the rust have appeared. Stems of all of the inoculated *P. strobus* seedlings remained healthy.

Thus despite all this concerted action toward verification of the presence of *C. ribicola* its presence in Japan remains conjectural.

It is most interesting that in Korea they find a rust similar to *C. ribicola* on *P. koraiensis*, in the absence of *Ribes* spp. (but not on *P. strobus* despite presence of rust-infected *Ribes*, see Bakshi, these proceedings).[3] Meanwhile in Japan we may have been able to inoculate *P. koraiensis* needles and stems with this "*C. ribicola*-like rust" from *Ribes* but not induce other than needle spots on *P. strobus*.

VOLE AND HARE DAMAGE TO WHITE PINES

Takahashi and Nishiguchi (1966) made laboratory tests of vole gnawing damage. In these tests, *P. griffithii* proved to be the most attractive to the red-backed vole--bark gnawing was severe. *P. strobus* and *P. monticola* were the next most severely gnawed, while *P. koraiensis* and *P. pentaphylla* were found to be rather unattractive (i.e., resistant to vole gnawing).

Earlier Takahashi and Iwamoto (1963) reported on rodent damage in the field. Seedlings of several species of conifers and broadleaved trees that were planted in a test area. Rodent damage was observed the next spring. Under snow cover, the bark of all but two species was gnawed by the red-backed vole. Moreover, the tops of all but 3 seedlings above the snow cover were gnawed by hares. The results of the field observation are

[3] *Editor's note: It has come to our attention quite recently that pathologists of the Korean Forest Research Institute near Seoul so far have unsuccessfully attempted inoculation of* R. mandshuricum *var.* villosum *Kom. with aeciospores similar to those of* C. ribicola *from the Korean* P. koraiensis *blister rust.*

shown in Table 2. The table shows that *P. strobus* proved attractive to voles in the field, as well as in the laboratory; also that in the field it was mildly attractive to hares.

Vole gnawing damage is one of the greatest problems in plantations of forest trees in Hokkaido, Japan. When the population level of the vole is low, *P. strobus* escapes gnawing damage, but when the level is high, *P. strobus* is severely gnawed. Therefore, control of voles must be obtained if *P. strobus* and many other introductions are to become important to forestry in Japan.

Table 2. Vole- and hare-gnawing of various tree species in the field, after Takahashi and Iwamoto (1963)

Species	Percentage of trees gnawed	
	By voles	By hares
Pinus strobus L.	39	7
P. sylvestris L.	98	6
Larix oglensis O. & S. var. *koreana* Ueki	11	3
L. leptolepis Gord.	89	5
L. gmelini (Rupr.) Litvin	0	0
Abies sachalinensis Mast.	0	0
Picea jezoensis (Sieb. & Zucc.) Carr.	2	0
Betula maximowicziana Regel	41	39
B. platyphylla Skat. var. *japonica* (Miq.) Hara	3	15

NEEDLE RUST SUSCEPTIBILITY AMONG WHITE PINES

Inoculation experiments using 8 species of white pines and inoculating with sporidia of 5 *Coleosporium* needle-rust species were made from 1959 to 1968 (Saho, 1968 and 1969). Results given in Table 3 show that *P. pumila* is quite resistant to all these species of needle rusts and that *P. pentaphylla* is resistant to 4 of the 5 rust species. On the contrary, *P. koraiensis* is highly susceptible to all 5 rusts, and *P. monticola* is moderately to highly susceptible to 4 of the 5 rusts.

Table 3. Relative susceptibility of native and introduced Japanese white pines to *Coleosporium* needle rusts

White pine species	Relative susceptibility[a] to five *Coleosporium* species				
Needle rusts	*C. cimicifugatum* Thüm	*C. eupatorii* Arthur	*C. neocacaliae* Saho	*C. neopetasitis* Saho	*C. neosenesionis* Saho
Native:					
P. koraiensis	++	+++	+++	+++	+++
P. pentaphylla	-	+	-	-	-
P. pumila	-	-	-	-	-
Foreign:					
P. cembra	-	++	+	+	-
P. griffithii	-	++	+	-	+
P. monticola	+	+++	+	++	+
P. peuce Griseb.	+	++	+	+	+
P. strobus	++	++	+	+	+

[a] Plus or minus susceptibility rankings have the following meaning: - = no peridermia (aecia) were found on needles (i.e., the thie pine host was resistant); + = few peridermia were found on needles (pine host moderately resistant); ++ = peridermia were recognized easily (pine host susceptible); and +++ = many peridermia were found on needles (pine host highly susceptible.)

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FLOOR DISCUSSION

Because this paper by H. Saho, along with the three preceding papers by S. K. Hyun, J. Ahsan and M.I.R. Khan, and P. D. Dogra, covered a group of related Asiatic white pines, important as sources of blister rust resistance, Moderator Bingham withheld floor discussion on the four papers until this time.

BINGHAM: Dr. Saho has just mentioned that *Pinus himekomatsu* of central Honshu may be a "threatened species" and in conversation last evening Dr. S. K. Hyun brought out the fact that there might be a similar threat to *Pinus armandii* in Taiwan. In view of this information the IUFRO Committee on White Pine Blister Rust is forwarding through its parent group (Dr. Gerhold's Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects) a recommendation that IUFRO

Section 22 initiate action to seek preservation of specimen stands of these species. Dr. Callaham, Leader of Section 22, is in the audience, so I'll ask him to remark on the protocol he will follow once he receives the recommendation from Dr. Gerhold.

CALLAHAM: Later today I am going to describe an FAO panel of experts on conservation of forest gene resources. One of the functions of this panel is to recommend international programs to preserve and conserve threatened species. The panel already has a tentative list of 7 or 8 of these species. The list needs additions and amendments. Dr. Gerhold's IUFRO Working Group should make a recommendation to this panel to add these species to the list. Your recommendations to the FAO panel should also be sent to the International Congress of the International Union for the Conservation of Nature (ICUN). It meets in India in the month of October. The ICUN produces a "Redbook" which lists all those species endangered or threatened with extinction. The FAO panel would like to add those species threatened with gene resource depletion to the list. In other words, a species might not be completely obliterated, but it might be so deteriorated genetically by man's practice that it is in danger. We would want to add this kind of endangered species to their list. I think there probably will be some action upon recommendations for addition of species at the ICUN meeting in India. The United States Forest Service will have a representative there (Dr. Stephen G. Boyce) who could represent us, or there may be others who would represent the concern of this group at the meeting in India. I would add at this point, that if anyone else knows any other threatened species that should be added to our list, please bring them to my attention during this meeting.

BINGHAM: As an old "white pine man" my enthusiasm was really aroused by seeing some of Dr. Hyun's color slides of a thinned plantation of *P. koraiensis*. Also, I was disappointed that neither Dr. Vidakovic who presented Ahsan and Khan's paper on *P. wallichiana* (syn. *P. griffithii*) in Pakistan, or Dr. Kriebel, who presented Dogra's paper on *Pinus wallichiana* in India, felt they had time to show slides of stands of that species. Having seen Ahsan and Khan's black and white photos, along with many of the colored slides of other European and Asiatic white pines, I am impressed with how really beautiful are these European and Asiatic white pine stands. Dr. Kriebel, among Dr. Dogra's slides of *P. wallichiana* you were able to show, I noticed some very strange, defoliated, roadside trees. Would you remark on these?

KRIEBEL: There were a couple of slides showing lopped branches, but I really can't tell you much about them.

BINGHAM: Dr. Mirko Vidakovic who is in the audience has returned only recently from an FAO Training Project at the Pakistan Forest Institute. Perhaps he can tell us about this lopping practice.

VIDAKOVIC: Perhaps Dr. Kedharnath can comment.

BINGHAM: I don't see Dr. Kedharnath, but perhaps Dr. Callaham can comment.

CALLAHAM: No, but it's quite common, to lop branches for fuel wood along those mountain trails.

BINGHAM: Having disposed of some generalities, the floor is hereby opened for questions addressed to the four individual panelists.

CALLAHAM: I should like to ask if anyone knows if isolated stands of Asian white pines on the offshore islands of Japan and Taiwan are remnants of ancient transfers by man or whether these truly are natural distributions?

HYUN: I know that the isolated distributions of *Pinus koraiensis* at high elevations in South Korea are natural, and it is also known that the distribution of *P. koraiensis* in north-central Honshu of Japan is natural.

SAHO: In respect to the distribution of *Pinus koraiensis* in Japan, yes, I think this is an isolated distribution. It covers less than 200 square kilometers, with a single outlier to the south at 34° latitude in Shikoku.

BINGHAM: But Dr. Saho, is there any question that this is not a natural stand of *Pinus koraiensis*?

SAHO: These are natural stands, and natural *Pinus koraiensis* is found nowhere else in Japan.

CALLAHAM: Is there no evidence that the species was established by man long ago?

SAHO: No. The earliest plantation was established in 1910.

VAN ARSDEL: Dr. Dogra isn't here, but I wondered if anybody knows anything about those eastern outliers of *Pinus griffithii* (*P. wallichiana* or blue pine).

KRIEBEL: I can give you a little more information than I was able to in covering Dr. Dogra's paper. Dr. Dogra mentions the northeastern blue pine (*P. griffithii*) found in some regions of Assam, areas in which there is an annual rainfall of 200 inches, as compared, for instance, with stands in areas of the upper Sutlej valley of northwestern India having 10 to 30 inches. He also states that the blue pines in northern Burma, on grassy slopes of several valleys in the upper Irrawadi River at elevations of about 4,900 to 6,900 feet, fall into his "moist upper level area", where growth is excellent. Perhaps you may be referring to those "little red X's", on Critchfield and Little's (1966) map 12, i.e., the area where *P. griffithii* overlaps with *P. armandii* in northeastern Burma. If so, I don't think Dr. Dogra gave any information on that area. You might be able to get some information from Dr. Chi-wu Wang's book, "The Forests of China."

VIDAKOVIC: I have a comment on Dr. Dogra's paper, where he considers incompatibility. When he refers to incompatibility between the provenances of *P. wallichiana*--I don't know but I have a feeling that it is only a question of time of ripening of the pollen and of pollination, not really compatibility.

KRIEBEL: I don't find that Dr. Dogra used the term incompatibility. He refers to reproductive barriers, and is talking about the differences in time of pollen shedding.

KEDNARNATH: A "functional compatibility barrier" might be a better term.

WHITE PINES IN NORTH AND CENTRAL AMERICA: *PINUS STROBUS* AND INTRODUCED ASIAN AND EUROPEAN SPECIES

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ABSTRACT

Adaptability, growth, insect resistance, and other characteristics of *P. strobus* (including var. *chiapensis*) and of European and Asiatic white pines in North America are discussed. Discussion of *P. strobus* includes its growth potential in both native stands and plantations.

Exotics described include *P. griffithii* (syn. *P. wallichiana*), *P. koraiensis*, *P. peuce*, *P. armandii*, *P. cembra*, *P. sibirica*, *P. parviflora* (including var. *pentaphylla*), and *P. pumila*.

Some of these species will be particularly useful as breeding material for the development of superior species hybrids. One species with good form and pest resistance which may have direct use after selection is *P. koraiensis*. *P. armandii* is very resistant to pests but introductions to date have not been very winter-hardy. Two particularly promising species are *P. griffithii*, desirable for its vigor, and *P. peuce*, a tree which seems to have great variation in resistance to white pine weevil injury. Both species are easily crossable with *P. strobus* and *P. monticola*, the two most important North American species.

Many of the hybrids have been more vigorous than either parent species in several test localities. Prospects appear good for future use of new hybrids with desirable combinations of vigor, form, and pest resistance.

EASTERN WHITE PINE

Pinus strobus L. is commonly known as eastern white pine and is the only white pine native to eastern North America. It is found in southern Canada from southeastern Manitoba to Newfoundland, in the Lake States, in scattered localities in the Midwest from Iowa to Ohio, in the northeastern United States, and south in the Appalachian Mountains to northern Georgia (Critchfield and Little, 1966).

Eastern white pine occurs naturally on a variety of soils, including coarse-textured tills, sandy soils, loams and silts. The species seems to require at least 20 percent of full sunlight for seedling survival under conditions of natural regeneration (Fig. 1). Early height growth



Figure 1. *Pinus strobus* stand with natural reproduction in the stand openings, Waushara County, Wisconsin (photo courtesy of Wisconsin State Department of Agriculture).

increases in proportion to light intensity above this point, unless some other factor becomes limiting. This early growth is comparatively slow, to about 1.5 m in the first 8 to 10 years (Fig. 1). During the subsequent 20 years, height growth of dominant trees may be rapid, sometimes 1 m but usually about 0.5 m per year (Figs. 1 and 2). The estimated yield of fully stocked, pure stands varies, depending on site index, from 8,000 to 38,000 board feet per acre[1] (110 to 530 m^3/ha) at 50 years, and from 40,000 to 78,000 board feet per acre (560 to 1100 m^3/ha) at 100 years (Wilson and McQuilkin, 1963).

Eastern white pine has a long life, commonly 200 to 300 years when undisturbed (Fig. 3), reaching a maximum height of about 65 m.

Growth of eastern white pine in plantations varies with seed source and planting locality. Early results of cooperative provenance tests (ages 3 to 8 years) showed that trees of southern and central Appalachian Mountain origins outgrew others in field tests in Georgia, North Carolina, Virginia, Kentucky, Ohio, Indiana, Illinois, Iowa, and lower Michigan (Sluder, 1963; Wright, Lemmien, and Bright, 1963; Funk, 1965; King and Nienstaedt, 1968). In two 13-year-old field tests in New England, local sources had the best survival and growth. The farther the collection was made from the test area and the more diverse the site and climate, the

[1] *International 1/2 inch rule.*



Figure 2. Young *Pinus strobus* stand in northern Wisconsin (photo courtesy of Wisconsin State Department of Agriculture).

poorer was the response of trees of that seed source in the test area (Pauley, Spurr, and Whitmore, 1955).

In other seed source tests in Wisconsin, Minnesota, Upper Michigan, and Ontario, the northern winter climate appeared to have adverse effects on trees of southern origins (King and Nienstaedt, 1968; Fowler and Heimburger, *unpublished data*).

Volume yields have been estimated in older plantations, but information on seed origin is usually not available. Yield per acre varies widely, increasing with age, site quality and spacing to at least 3 x 3 m (Vimmerstedt, 1962; Gilmore, 1968). In the southern Appalachians, yield is as high as 55,000 board feet per acre (770 m^3/ha) at 35 years under the most favorable conditions (Vimmerstedt, 1962).

P. strobus grows well in plantations in the midwestern United States, where natural disjunct stands are restricted to cool microclimates. In this region, it seems to be adapted to a variety of sites, except heavy, poorly drained soils and strip mine spoil banks.

P. strobus does not seem to be well adapted in places where it has been planted in western North America. Growth has been poor at Placerville, California, in the Sierra Nevada mountains. Form in Montana plantations is poor (Barnes and Bingham, 1962). Average diameter of 50-year-old plots in one Montana plantation was 24 to 30 cm (Barnes, *unpublished data*).



Figure 3. An old stand of *Pinus strobus* on a recreation area in Adams County, Wisconsin (photo courtesy of the Wisconsin State Department of Agriculture).

The principal destructive agent of *P. strobus*, other than blister rust, is the white pine weevil, *Pissodes strobi* (Peck). This insect kills the terminal shoot and deforms most trees in the Northeast (Fig. 4). It also does much damage in the Lake States and Canada but is not a serious pext in the southern Appalachians (Kulman and Harmann, 1965) and the Midwest. Extensive planting of white pine in some areas where there is presently no problem could conceivably cause an increase in the weevil population and could result in widespread damage. The serious economic loss in northeastern white pine stands resulting from weevil attack has stimulated efforts to select and breed for resistance to weevil injury. Early results indicate that weevil-resistant white pines may be developed either through selection in *P. strobus* (Stroh and Gerhold, 1965) or by interspecific hybridization (Wright and Gabriel, 1959; Heimburger, 1963).

Chlorotic dwarf is a disease common in young plantations throughout the midwestern and eastern United States. The cause is now known to be air pollution; the response is apparently genetically controlled (Dochinger and Seliskar, 1970).

In pure stands, eastern white pine nearly always differentiates into a wide range of crown and diameter classes due to inherent variation in vigor (Deen, 1933). Because the species has a tendency to retain the lower branches after they die, pruning is necessary to obtain knot-free lumber (Fig. 1). Apical dominance is pronounced and unweeviled trees

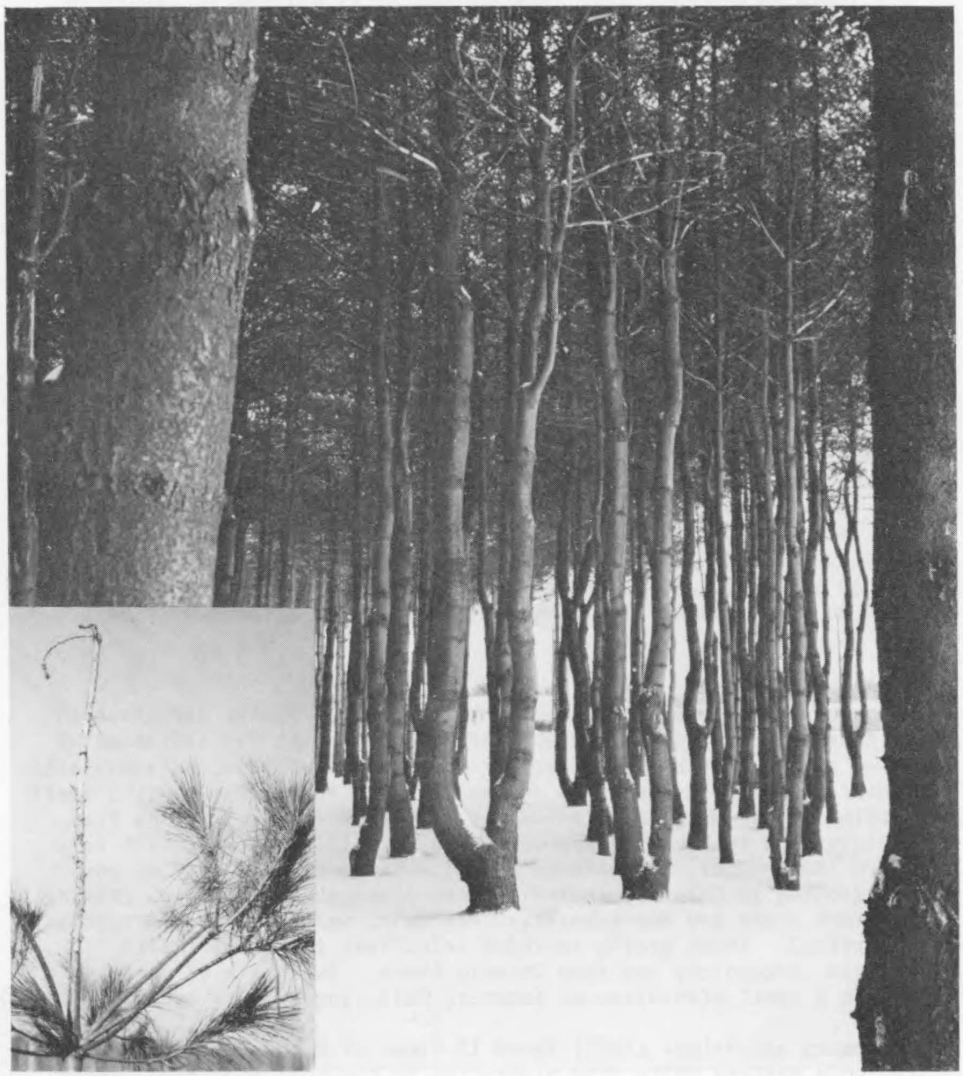


Figure 4. A 20+-year-old plantation of *Pinus strobus* near North Hampton, New Hampshire, that has been attacked repeatedly by the white pine weevil *Pissodes strobi* (photo by U.S. Dept. Agric., Forest Service, Northeastern Forest Experiment Station, Durham, N. H.). Insert shows a young *P. strobus* leader one year after attack by *P. strobi* (photo by R. G. Miller, Rhinelander, Wisc.).

usually have a straight bole. Genetic selection for stem form is therefore less important than is selection for vigor and pest resistance.

White pine is a high-quality wood for many lumber products because of its light weight, strength, straight grain, and excellent machining properties (Brown, Panshin, and Forsaith, 1949).

A taxon of assumed close relationship to *P. strobus* is native to central America. Though Critchfield and Little (1966) have continued the earlier listing of this tree as *P. strobus* var. *chiapensis* Martínez, Andresen's (1964) study appears to justify its elevation to the rank of species with the name *P. chiapensis* (Martínez) Andresen. The natural distribution is in Guatemala and Mexico on warm-temperate mountain slopes and ridges with frequent fogs and sea winds, at elevations between 800 and 1200 m (Andresen, 1964; Rzedowski and Vela, 1966). Chiapas pine is not winter-hardy in the northern parts of the United States (Wright, 1958; Kriebel, *unpublished data*).

INTRODUCED ASIAN AND EUROPEAN SPECIES

P. GRIFFITHII MCCLELL. (SYN. *P. WALLICHIANA* A.B. Jacks.)

Some of the earliest introductions of the Himalayan white pine (blue pine), *P. griffithii*, into North America were in the Philadelphia area, where there are numerous specimens over 70 years old. Most of the older trees are still growing vigorously; some are 20 to 25 m tall and 0.5 to 1.0 m in diameter. There are other old specimens in southeastern and western New York state (Wright, 1958). Older trees are also growing in Maryland and New Jersey (Fig. 5A), where the winter climate is better suited to survival. In recent seedling studies in Maryland, *P. griffithii* has had an early growth rate comparable to that of *P. strobus* (Genys, 1965).

Introduced Himalayan white pine has varied in winter hardiness in North America, possibly as a result of differences in the elevation of the seed source. It has been seriously injured at Boston, Massachusetts, by winter cold and severe winds (Wyman, 1965). In Ontario, only a small proportion of the material planted has survived. Grafted scions from high elevations in Pakistan are very hardy but inferior in growth rate and form (Heimburger, *unpublished notes*). There are a number of good clones growing in Ontario, including some propagated from trees growing in New York state and Massachusetts. In Ohio, very few grafted specimens have survived. These grafts included selections from Placerville, California accessions and from Ontario trees. Two trees of seedling origin in a small plantation at Wooster, Ohio, survived to age 45 (Fig. 5B).

Lemmien and Wright (1963) found 13 trees of *P. griffithii* in a 32-year-old eastern white pine plantation in southern Michigan. These trees grew at about the same rate as the eastern white pine, but there was about 3 times as much damage due to *Pissodes strobi* in the Himalayan as in the native species. This observation of susceptibility to weevil damage supports earlier observations by Heimburger (1958) in Ontario. It is a trait which may limit the direct use of *P. griffithii* for forest planting in parts of the range of eastern white pine. Susceptibility to pales weevil, *Hylobius pales* (Herbst), is comparable to that of *P. strobus* (Santamour and Rhodes, 1966).



A. B.



C. D.

Figure 5. A. *Pinus griffithii* at Westfield, New Jersey, with a heavy cone crop. B. Forty-five-year-old *P. griffithii* at the Secrest Arboretum, Wooster, Ohio. C. Thirty-four-year-old *Pinus koraiensis* at the Westtown Arboretum, Westtown, Pennsylvania (near Philadelphia). D. Thirty-four-year-old *Pinus peuce* at the Westtown Arboretum.

Himalayan white pine survives and grows well in the vicinity of Seattle, Washington (Wyman, 1965). It outgrows *P. monticola* in the Sierra Nevada mountains of California but is not as drought resistant as the western white pine (Duffield and Righter, 1953).

The species is a very attractive ornamental because of its long drooping needles and spreading branches (Fig. 5A and Wright, 1958). Pruning is necessary, however, if timber is the objective. Of greater interest to American tree breeders is its breeding value for the introduction of vigor and disease resistance into hybrids with native American white pines.

P. KORAIENSIS SIEB. & ZUCC.

P. koraiensis, Korean white pine, is probably one of the hardiest of the white pines. Growth rate varies widely; some specimens in the northeastern United States have grown only a few to several centimeters per year (Fig. 5C), whereas other have averaged over 0.5 m in annual height growth. The bole form is usually good. One of the best specimens of Korean white pine in the Northeast is at Williamstown, Massachusetts. At age 35, the tree was 18 m tall, 25 cm in diameter and had a perfectly straight trunk (Wright, 1958; Wright and Gabriel, 1959).

At Wooster, Ohio, height and diameter growth of *P. koraiensis* trees planted on a 2 x 2 m spacing has been slightly less than that of *P. strobus* in similar plots nearby. At age 20, average height was 8 m and average diameter 10.5 cm (Aughanbaugh, Muckley, and Diller, 1958). At age 54, 2 of 49 trees remain. One is 21 m high and 30 cm in diameter, while the other is only one third as large.

Studies in the northeastern United States and Canada indicate that Korean white pine has a high degree of resistance to attack by the white pine weevil (Wright and Gabriel, 1959; Heimburger, *unpublished data*). This characteristic is in itself sufficient inducement for field testing of growth characteristics and adaptability as related to genotype.

P. PEUCE GRISEB.

P. peuce, the Balkan or Macedonian white pine, is hardy throughout most of the United States and southern Canada. It has a dense, narrow crown, fine branches, and a straight bole with little taper.

Growth is slow to moderate, usually about 0.3 m per year in the northeastern and midwestern states during the first 2 or 3 decades (Fig. 5D and Wright and Gabriel, 1959; Aughanbaugh, Muckley, and Diller, 1958; Heimburger, *unpublished notes*). One of the oldest Balkan pines in the United States is growing near Boston. It was 15 m tall at age 80 and had a spread of 4.6 m (Wyman, 1965).

About 1951, A. G. Johnson showed me one *P. peuce* tree in the Arnold Arboretum near Boston that had withstood repeated attacks by the white pine weevil, though surrounding trees of *P. peuce* and *P. strobus* were severely damaged. Resistant trees of Balkan white pine have also been found in Ontario. Resistance is apparently the result of heavy resin flow and subsequent healing of the puncture wounds (Fowler and Heimburger, 1958; Heimburger, 1958, 1963). Field observations by Wright and Gabriel

(1959) in New York state showed that there were far fewer weevilings per tree on *P. peuce* than on *P. strobus*.

Santamour (1965a,b; 1967) studied insect-induced crystallization of white pine resins as a possible criterion for resistance assessment. His results suggested that at least two of the species which should be used in any *Pissodes*-resistance breeding program, namely *P. monticola* and *P. peuce*, may also contribute some degree of resistance to the white pine cone beetle, *Conopthorus coniperda* Sz.

Balkan pine may also be a useful species for planting in regions where air pollution is a problem. Greenhouse studies by gas exchange analysis showed that *P. peuce* needles had a higher level of SO_2 tolerance than did needles of *P. sylvestris*. This was not the case with *P. strobus* (Enderlein and Vogl, 1966).

P. ARMANDII FRANCH.

Armand pine, *P. armandii*, has not been widely planted in North America, possibly because it is not as winter-hardy as many of the other white pines. Young specimens at the Morris Arboretum near Philadelphia grew rapidly but developed crooks as a result of winter dieback. The species has survived at Rochester, New York, where the trees have poor form and have grown at the rate of about 0.3 m in height per year (Wright and Gabriel, 1959), and at the Morton Arboretum near Chicago, where three specimens were 3.5 to 6.0 m in height at age 25. One had multiple stems (R. M. Nordine, *personal communication*). Grafts from these trees have not survived in northern Ohio. In a test in Arkansas, only 20 percent of a small group of seedlings was alive at age 2 (Schmitt and Namkoong, 1965). Armand pine has survived at Placerville, California (Liddicoet and Righter, 1960) but the trees are in poor condition (R. J. Steinhoff, *personal communication*).

Because of the wide elevational and geographical distribution of the species in Taiwan and southwestern and southcentral China, it is possible that hardier genotypes could be introduced into North America. Armand pine is found at altitudes as high as 3,500 to 4,000 m in the spruce-fir belt of western Szechwan province (Wang, 1961).

The scanty evidence available indicates that the species is of more interest as an ornamental and a source of blister rust resistance than as a timber tree. It has a rather open crown, with wide-spreading branches (Fig. 6A). The apparent barrier to crossing with any species but *P. lambertiana* may preclude the use of its hybrids in regions with a cold winter climate. The species seems, however, to merit further testing if seed collections can be obtained.

P. CEMBRA L. AND *P. SIBIRICA* DU TOUR.

The Swiss and Siberian stone pines have often been considered to be varieties or races of a single species. They are winter-hardy throughout most of the United States and at least as far north as Dropmore, Manitoba, in Canada at latitude 51°N. (Rehder, 1949; Wyman, 1965). Both species are very slow-growing in North America and of little value for timber production. A specimen of *P. cembra* in New York state was 100 years old and 18 m tall in 1957; another was 80 years old and 12 m tall



A.



B.



C.



D.

Figure 6. A. Thirty-eight-year-old *Pinus armandii* at Westtown, Pennsylvania. B. *Pinus cembra* at Mt. Auburn, Massachusetts (photo courtesy of Arnold Arboretum). C. Forty-seven-year-old *Pinus parviflora* (probably var. *pentaphylla*) at Westtown, Pennsylvania. D. Fifty-three-year-old *P. parviflora* (probably var. *himekomatsu*) at Wooster, Ohio.

(Wright, 1958). *P. sibirica* is a taller tree than *P. cembra*, with shorter leaves and larger cones (Rehder, 1949). Both species are suitable as ornamentals where a slow-growing tree of dense habit is desired (Fig. 6B and Wyman, 1965).

P. PARVIFLORA SIEB. AND ZUCC.

Japanese white pine is slow-growing in North America and usually has a poor form for timber (Fig. 6C and D, and Wright, 1958). The northern variety *pentaphylla* is a straighter form that might have some possibilities for breeding (Fig. 6C). A 40-year-old specimen at Rochester, New York, apparently of the *pentaphylla* variety, was 15 m tall and 38 cm in diameter at age 40. The species is susceptible to the white pine weevil and therefore has little promise as a forest tree for most of the Northeast (Wright and Gabriel, 1959).

P. PUMILA REGEL

The Japanese stone pine, *P. pumila*, is considered by recent investigators to be more closely allied to *P. parviflora* than to the *P. cembra*-*P. sibirica* group (Ferré, 1960; Malyshev, 1960). It is a shrubby form of no timber value, though Heimburger (*unpublished notes*) believes that it may be of breeding value because of resistance to sulfur dioxide injury.

HYBRIDS OF *P. STROBUS* AND EUROPEAN AND ASIATIC SPECIES

In addition to natural hybrids, many different white pine hybrids have been obtained by artificial crossing (Righter and Duffield, 1951; Riker and Patton, 1954; Heimburger, 1958; Wright, 1959). These hybrids have been tested in most parts of the United States and southern Canada (Southeastern Forest Experiment Station, 1950; Righter and Duffield, 1951; Wright, 1959; Fowler, *unpublished data*; Kriebel and Fowler, 1965). Botanical descriptions have been prepared for many of them (Keng and Little, 1961; Little and Righter, 1965), though some of the descriptions do not fully agree with observations of specimens from different parents or of the same biotypes growing in different localities. Apparently parental genotype and test environment can affect both morphological and physiological responses of white pine hybrids (Kriebel and Fowler, 1965).

Some of the hybrids can outgrow either parent, at least in the early years. An example is *P. monticola* x *strobus* in the Northeast (Wright, 1959) and the Northwest (Bingham, Squillace and Patton, 1956). However, records of hybrid vigor in the Northwest are based on nursery growth. Later performance in the field has varied. In Idaho, *P. monticola* x *strobus* hybrids were taller than *P. monticola* trees with the same female parents 10 years after outplanting. But in western Montana, snow damage was severe to hybrid progenies as well as to progenies of both *P. monticola* and *P. strobus* (Barnes and Bingham, 1962; R. J. Steinhoff, *personal communication*).

Other combinations with early hybrid vigor are *P. griffithii* x *strobus*, *P. strobus* x *griffithii*, *P. flexilis* x *griffithii*, *P. monticola* x *griffithii*, *P. ayacahuite* x *griffithii*, *P. ayacahuite* x *strobus*, and *P. strobus* x *ayacahuite* (Wright, 1959). *P. strobus* x *griffithii* is more vigorous than *P. strobus* in northern Ohio and more winter-hardy than *P. griffithii* (Kriebel, 1963).

P. peuce hybrids, though not exceptionally vigorous, are of special interest because of the excellent form, rust resistance and possible weevil resistance of this species (Wright and Gabriel, 1959; Heimburger, 1958, 1963). At least 7 different crosses between *P. peuce*, *P. strobus*, and their hybrids have been made successfully, mostly at Maple, Ontario. The hybrid *P. peuce* x *strobus* was considered by Fowler and Heimburger (1958) to be of doubtful value to forestry because of its intermediate growth rate, but valuable for back crossing to *P. strobus* to introduce resistance to blister rust and weevil damage. Successful crosses have also been made between *P. monticola* and *P. peuce*, and between *P. monticola* and the hybrid *P. peuce* x *strobus* (Wright, 1959).

Korean white pine hybrids with sugar pine *P. lambertiana*) are considered by Heimburger (*unpublished notes*) to be worth further study from the standpoint of weevil resistance as well as blister rust resistance. Kriebel found that the barrier to hybridity in crosses of *P. strobus* x *koraiensis* is a problem of embryo inviability rather than gametic incompatibility. The same situation exists in the crosses *P. strobus* x *cembra*. *P. strobus* x *flexilis* (Kriebel, 1968), and probably also *P. peuce* x *cembra* (Hagman and Mikkola, 1963). Because some cell differentiation is possible in the zygote, there is a possibility of finding ways to obtain new and very useful hybrids.

SUMMARY

In addition to eastern white pine, several European and Asiatic species of white pines appear to be useful in North America because of their vigor or pest resistance. The high degree of crossability of some of these species offers the attractive possibility of developing vigorous hybrids on a large scale, and of introducing insect and disease resistance into the native *P. strobus*. The white pines, in fact, seem to be particularly well suited to the application of interspecific hybridization as a technique for forest tree improvement. Prior to mass production, however, is the most urgent need for the scientific study of variation within each of the potential parent species by cooperative international testing, and the subsequent selection, within the areas of potential use, of superior genotypes to be used for the breeding of hybrids.

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FLOOR DISCUSSION

Moderator Bingham withheld discussion on this paper so that it could be discussed with Dr. Steinhoff's closely related paper which follows.

WHITE PINES OF WESTERN NORTH AMERICA AND CENTRAL AMERICA

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ABSTRACT

Both species of foxtail pines (Subsection *Balfourianae*, Section *Parrya*, Subgenus *Strobus*) grow in western North America. *Pinus balfouriana* has a very restricted distribution while *P. aristata* is widely distributed. Neither species is commercially important but both have high esthetic value and may be useful for watershed protection or avalanche control.

There are six species of white pines (Section *Strobus*, Subgenus *Strobus*) native to western North America and Central America. All of these species are rather widely distributed with one or more species occurring in most of the major mountain ranges. Although any of the species may occur in pure stands, they usually are found mixed with several other coniferous species.

Three of the species, *P. ayacahuite*, *P. lambertiana*, and *P. monticola*, are commercially important and a fourth, *P. strobiformis* is harvested, but on a much smaller scale. The other two species, *P. albicaulis* and *P. flexilis* are not often cut for timber but have esthetic value and are important for watershed protection.

Numerous efforts have been made throughout the world to cross these species with other white pines. Several of the resulting hybrid combinations show promise for a variety of uses and for planting in areas where there are few or no native white pines.

INTRODUCTION

Subgenus *Strobus* of the genus *Pinus* has 8 representatives in western North America including species in both of the Sections *Strobus* and *Parrya*.

In Subsection *Balfourianae* of Section *Parrya*, 2 species are represented--*Pinus balfouriana* Grev. and Balf., foxtail pine, and *Pinus aristata* Engelm., bristlecone pine.

Both subsections of Section *Strobus* are represented in western North America. Subsection *Cembrae* is represented by a single species, *Pinus albicaulis* Engelm.; Subsection *Strobi* by species and varieties as follows: *Pinus flexilis* James; *Pinus strobiformis* Engelm.; *Pinus ayacahuite* Ehrenb.;

Pinus lambertiana Dougl.; *Pinus monticola* Dougl.; and *Pinus strobus* var. *chiapensis* Martínez. The latter variety is covered by H. B. Kriebel, elsewhere in these proceedings.[1] Three of these species--*P. albicaulis*, *P. flexilis*, and *P. monticola*--are limited to Canada and the United States. Two, *P. lambertiana* and *P. strobiformis*, occur in both the United States and Mexico. Another, *P. ayacahuite*, is found from central Mexico southward into the Central American countries of Guatemala, El Salvador, and Honduras.

SECTION *PARRYA*

SUBSECTION *BALFOURIANAE*

Foxtail Pine (*P. balfouriana*) and Bristlecone Pine (*P. aristata*)

Foxtail pine has a very limited distribution in two parts of California (Critchfield and Little, 1966; Map 20). Bristlecone pine is more widely distributed in east-central California, eastern Nevada, Utah, Colorado, and northern New Mexico and Arizona (Critchfield and Little, 1966; Map 21). When cut for study, one bristlecone pine tree in eastern Nevada proved to be at least 4,844 years old, making it the oldest known tree (Currey, 1965). Trees of both of these species are very slow growing (3 to 6 inches height per year) and of no commercial value for timber production (Figs. 1 and 2).

The two species, foxtail and bristlecone pines, have been successfully crossed at the Institute of Forest Genetics, Placerville, California. Attempts to cross these species with members of Section *Strobus* have been very limited (Institute of Forest Genetics, Placerville, Calif., *unpublished data*; and Bingham, Hoff, and Steinhoff, *In press*), but it appears unlikely that they will hybridize. Because of their very slow growth these species probably would be of interest only to someone working on trees suitable for watershed protection or avalanche control, although *P. aristata* appears to be fairly resistant to attack by the blister rust fungus (*Cronartium ribicola* J. C. Fisch. ex Rabenh.; see Bingham[2]).

SECTION *STROBUS*

SUBSECTION *CEMBRAE*

Whitebark Pine (*P. albicaulis*)

This species has a range extending from central British Columbia on the north to the southern Sierra Nevada Mountains in California. In the Rocky Mountains, it extends as far south as central Wyoming (Critchfield and Little, 1966; Map 5). It occurs primiarly near timberline but in the north occasional trees may be found scattered at lower elevations.

Whitebark pine, as found growing naturally, usually is of limited value for timber production but is important for watershed protection and has considerable esthetic value. Because of their normally exposed habitat, most trees are twisted and repeatedly forked and frequently are somewhat procumbent. The limbs are large, upturned sharply, and often compete with the main stem for dominance (Fig. 3). Under more favorable

[1] *Kriebel, H. B. White pines in North and Central America:* Pinus strobus *and introduced Asian and European species, these proceedings.*

[2] *Bingham, R. T. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines, these proceedings.*



Figure 1. *Pinus balfouriana* in the Sierra Nevada Mountains of California (U.S. Forest Service photo).



Figure 2. *Pinus aristata* in the White Mountains of California (U.S. Forest Service photo).



Figure 3. Typical form of *Pinus albicaulis* in the Rocky Mountains in southwestern Montana (U.S. Forest Service photo).

conditions, some individuals develop to a size and shape suitable for timber production (Fig. 4). Day (1967) reported a whitebark pine 107 feet tall and 31 inches in diameter in the Crowsnest Forest in southwestern Alberta. He also reported stands containing trees over 90 feet tall and up to 36 inches D.B.H. in two areas of British Columbia. A stand of whitebark pine growing in the Kaniksu National Forest in northern Idaho also contained many large trees, most of which have been cut for timber.

Planting of whitebark pine has been limited to special purposes such as in arboreta. The finding of occasional large, timber-type trees indicates that selection for desirable types is possible, although the species is extremely susceptible to white pine blister rust disease (Bingham[2]).

Attempts have been made to cross *P. albicaulis* with most species of subsections *Cembrae* and *Strobi*. Crosses with *Pinus cembra* L., *Pinus pumila* Regel, *Pinus sibirica* Du Tour, *P. flexilis*, and *P. monticola* have yielded seed or seedlings but the putative hybrids are not yet large enough for verification (C. Heimburger, *personal communication, P. cembra* and *P. sibirica*; Institute of Forest Genetics, Placerville, Calif., *unpublished data, P. cembra, P. pumila, P. flexilis*; Bingham, Hoff, and Steinhoff, *in press, P. monticola*).

SUBSECTION *STROBI*

Limber Pine (*P. flexilis*)

Limber pine is another widely distributed white pine. It is found throughout the Rocky Mountain chain from southern Alberta and British Columbia to southern Colorado and north-central New Mexico. It is also found in the mountains of south-central and southeastern Idaho and in Nevada and Utah with a possible extension to north-central Arizona. In California it occurs in the Sierra Nevada Mountains in the east-central



Figure 4. Better formed *Pinus albicaulis* trees in Yellowstone National Park, Wyoming (U.S. Forest Service photo).

part of the state and in several mountain ranges in the southwestern part. There are a few scattered trees in northeastern Oregon and west-central Idaho. It is also found in isolated spots in western North and South Dakota and southwestern Nebraska (Critchfield and Little, 1966; Map 8). In areas where the elevational range is sufficient the species often has a split distribution, growing with *Juniperous* spp. on droughty sites in the transition zone between grassland and forest as well as with *P. albicaulis*, *Picea engelmannii* Parry, and *Abies lasiocarpa* (Hook.) Nutt. at upper timberline.

Limber pine is seldom harvested on a commercial basis but some trees have been used for rough lumber and mine timbers in areas wnere other trees are scarce. The species has esthetic importance in places such as Craters of the Moon National Monument in southern Idaho where it is the only tree occurring over much of the area. Limber pine also provides valuable watershed protection in many areas.

Naturally occurring limber pines usually have widely rounded crowns that often contain several stems or upturned branches (Fig. 5). The mature trees usually range from 30 to 50 feet in height with diameters of 1.5 to 3 feet. Maximum reported height is 85 feet (Harlow and Harrar, 1950) and maximum diameter 7.5 feet (Littlecott, 1969).

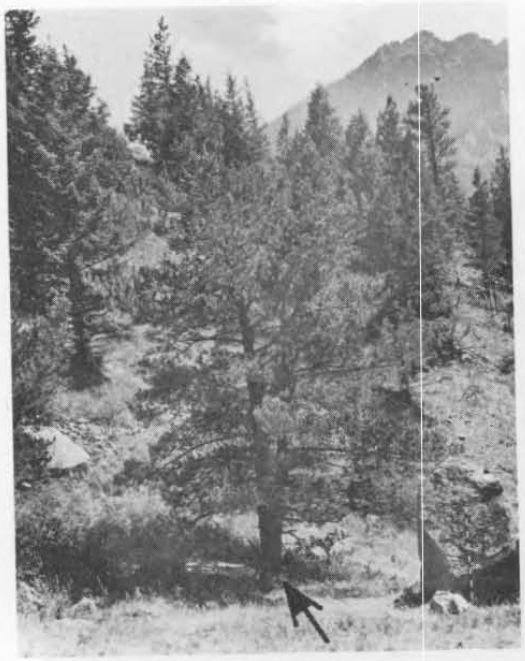


Figure 5. Mixed stand containing *Pinus flexilis* (arrow) near Billings, Montana (photo courtesy J. W. Andresen).

Limber pine has been planted in arboreta and experimental plots but no plantings have been made on a commercial scale. A group of 4 trees at the Institute of Forest Genetics in Placerville, California, averaged 42 feet tall and 11 inches in diameter at 32 years of age (Institute of Forest Genetics, Placerville, Calif., *unpublished data*). Wright (1958) reported that some limber pines in Philadelphia were growing faster than eastern white pines (*Pinus strobus* L.) planted nearby. A 24-year-old tree in Wooster, Ohio, is 37 feet tall and 6 inches in diameter (H. B. Kriebel, *personal communication*). Several provenance test plantations recently have been established in the north-central United States from stock grown at Michigan State University. While many of the trees present in arboreta and parks are multistemmed, others indicate that trees suited to lumber production could be obtained with proper selection. The species appears to be moderately to highly susceptible to the white pine blister rust disease (Bingham[2]).

Limber pine has been successfully crossed with *P. strobiformis* and *P. monticola* (Little and Righter, 1965); and with *P. ayacahuite*, *Pinus griffithii* McClell. (syn. *P. wallichiana* A.B. Jacks.), and *P. strobus* (Wright, 1959). A cross with *P. albicaulis* produced two seedlings which gave indication of being hybrids but they were accidentally destroyed before verification could be completed (W. B. Critchfield, *personal communication*). The *P. flexilis* x *P. griffithii* hybrids at Placerville were 11 feet tall at 10 years (Little and Righter, 1965).

Southwestern White Pine (*P. strobiformis*)

This species has been the source of considerable taxonomic controversy since its discovery. Synonymous names are *P. flexilis* var. *reflexa* Engelm. and *P. ayacahuite* var. *brachyptera* Shaw. Southwestern white pine is distributed from southern Colorado and extreme southern Utah through Arizona, New Mexico, and western Texas in the U.S.A. and Sonora, Chihuahua, Coahuila, Sinaloa, Durango, Zacatecas, Nuevo Leon, and Tamaulipas to San Louis Potosi in Mexico (Critchfield and Little, 1966; Map 8).

Individual trees of the species are quite variable depending on the conditions under which they grow. Trees on exposed sites often have multiple-stemmed crowns or broad crowns with upturned branches. On more protected sites where they are competing with one another and with other species the trees are usually single stemmed and of a conical shape (Fig. 6). Single, mature specimens may be 4 feet or more in diameter and 100 feet tall (Loock, 1950; Sargent, 1897). The species is harvested along with other species in timber sales in Arizona and New Mexico. In Mexico it is used for furniture, pattern-making, and other interior uses (Loock, 1950).



Figure 6. Open-grown *Pinus strobiformis* near Springerville, Arizona (photo courtesy J. W. Andresen).

Southwestern white pine is not planted commercially in the United States. It has been tried in mixed plantations in the Union of South Africa and does well where conditions are favorable (Loock, 1950). Streets (1962) reported that individuals in the best South African plantation averaged 34 feet in height and 8 inches in diameter 16 years after outplanting.

Two trees in the arboretum at Placerville, California, average 38 feet tall and 7 inches in diameter at 29 years of age (Institute of Forest Genetics, Placerville, Calif., *unpublished data*). Seedlings from several United States sources have been planted in the same provenance trials with limber pine, in the north-central states. Provenance plantings of 20 additional sources were made in the north-central states and in Arizona, Utah, California, and Idaho in 1967, but initial survival has been poor.

Pinus strobiformis has been crossed successfully with *P. flexilis* and *P. monticola* (Little and Righter, 1965). Young hybrid *P. monticola* x *P. strobiformis* trees at Placerville were 12 feet tall at 12 years of age (Little and Righter, 1965). They are intermediate in height between seedlings of the parental species.

Southwestern white pine appears to have considerable potential for planting outside its natural range. Once established it appears to be winter hardy in the north-central states, California, and Idaho. It also appears to have promise in hybrid combinations. Its relative blister rust resistance is in question. Bingham[2] places it among "species deserving more attention," saying that "resistance appears to be well above expectation,...and needs to be confirmed."

Mexican White Pine (*P. ayacahuite*)

Mexican white pine is distributed from the Mexican states of Jalisco and Hidalgo southeastward to Guatemala, El Salvador, and western Honduras (Critchfield and Little, 1966; Map 9). The species is considered by many (Shaw, 1909; Martinez, 1948; Loock, 1950) to be composed of two varieties. The type variety is found mostly in southern Mexico and Central America. The variety *veitchii* Shaw is restricted to central Mexico (Loock, 1950). Differences between the varieties are restricted primarily to cone and seed characters and are not concerned with the growth or form of the trees.

One of the best timber trees of Mexico, Mexican white pine grows to heights of 140 feet or more and diameters up to 5 feet (Loock, 1950). It does best on deep moist soils. This species usually occurs as scattered individuals in a mixture with other species so the volume per unit area is not very high.

Pinus ayacahuite is planted in Mexico and has been tried in a forest plantation in the Union of South Africa (Loock, 1950). At 25 years in South Africa the trees averaged 11.5 inches in diameter and 65 feet in height (Streets, 1962).

Trees up to 80 feet tall have been reported in British arboreta (Dallimore and Jackson, 1967) and a specimen 26 inches in diameter in Pennsylvania was reported by Wright (1958). Three trees at Placerville, California, averaged 34 feet in height and 8 inches in diameter at 36 years (Institute of Forest Genetics, Placerville, Calif., *unpublished data*).

The first known hybrids involving Mexican white pine resulted from spontaneous crossing with *P. griffithii* in the arboretum at Westonbirt, Great Britain (Jackson, 1933). These hybrids, *P.* x *holfordiana* A.B. Jacks., were 70 to 80 feet tall at 50 years of age (Dallimore and

Jackson, 1967). Additional hybrids with *P. flexilis* and *P. strobus* have been reported by Wright (1959). There is some question about the identity of the *P. ayacahuite* trees used in making the last two hybrids listed above. It is possible that these trees may themselves be hybrids, i.e., *P.* x *holfordiana* (J. W. Andresen, *personal communication*).

Mexican white pine would appear to have very good potential for planting as a timber tree in areas where the climate is moderately warm and moist. The *P. ayacahuite* x *griffithii* hybrid also appears to have considerable potential for slightly cooler areas. The relative blister rust resistance of *P. ayacahuite* is largely unknown (Bingham[2]).

Sugar Pine (*P. lambertiana*)

Sugar pine is the largest of the white pines, reaching heights to 250 feet and diameters of 10 feet (Fowells, 1965). It is native to the mountain ranges of west-central and southwestern Oregon, California, extreme west-central Nevada, and a small area in northern Baja California in Mexico (Critchfield and Little, 1966; Map 7). Best growth is obtained on deep, well-drained soils in areas where the annual precipitation is 40 to 50 inches per year. The species most often occurs over an elevation range of 3,000 to 5,000 feet; however, the extreme lower limit is about 1,000 feet in western Oregon and the extreme upper limit is about 10,500 feet in southern California and Baja California (Fowells, 1965).

Sugar pine usually occurs in mixed stands with a wide variety of other species including: *Pinus ponderosa* Laws., *Pinus jeffreyi* Grev. & Balf., *Abies magnifica* A. Murr., *Abies concolor* (Gord. and Glend.) Lindl., *Abies procera* Rehd., and *Pseudotsuga menziesii* (Mirb.) Franco. Single, large, old trees may contain 25,000 board feet of lumber or more but the average yield per acre would probably not be much over 50,000 board feet of sugar pine (Fig. 7). In well-managed young stands on the best sites, yields of 85,000 board feet per acre are expected at 100 years (Fowells, 1965) (Fig. 8). On medium sites, dominant young trees reach 100 feet in height and 21 inches in diameter at 100 years. On high-quality sites they are slightly taller and about the same diameter at 60 years (Fowells, 1965).

Sugar pine is planted on a commercial scale in Oregon and California and also has been tried in several countries around the world. New Zealand has some 180 acres of plantations with growth ranging from moderate to good, i.e., 90 feet tall and 25 inches in diameter at 48 years (Streets, 1962). However, it appears that few, if any, of the countries that have experimented with sugar pine plan any large scale plantings because of establishment difficulties and restrictive site requirements for good growth.

Attempts to cross sugar pine with other species have been successful only with *Pinus armandii* Franch. and *Pinus koraiensis* Sieb. & Zucc. (Righter and Duffield, 1951). Practical interest in the hybrids has been related to the possibility of introducting blister rust resistance. The significance of these crosses from a taxonomic and evolutionary point of view is also of prime interest.

Although sugar pine is an important and productive tree in its natural habitat it has not found too much favor in trials elsewhere. This is perhaps due to its site requirements for good growth; also, the species is highly susceptible to the white pine blister rust disease (see Bingham[2]).



Figure 7. Mature *Pinus lambertiana* in a mixed stand in California (U.S. Forest Service photo).



Figure 8. *Pinus lambertiana*--40-year-old plantation at the Institute of Forest Genetics, Placerville, California (U.S. Forest Service photo).

Western White Pine (*Pinus monticola*)

Western white pine occurs naturally from southeastern British Columbia and extreme southwestern Alberta southward into northwestern Montana, northeastern Washington, and northern Idaho to northeastern Oregon. Further west it occurs from southwestern British Columbia southward through western Washington and Oregon, northern California, and extreme west-central Nevada to the southern Sierra Nevada Mountains of California (Critchfield and Little, 1966; Map 6).

In the northern part of its range western white pine has a broad elevational spread--about 5,000 feet--but further south the spread is restricted to about 1,500 feet (Wellner, 1962). The species generally requires fairly moist sites, i.e., areas with 35 to 40 inches of precipitation annually or, in drier areas, stream bottoms or north slopes. Western white pine is a fire-perpetuated seral species in most areas. It commonly occurs in mixed stands, but is also found in essentially pure stands.

Western white pine grows slowly during its first 10 to 15 years but then maintains a rapid growth rate for several decades, reaching heights up to 220 feet and diameters to 7 feet (Pomeroy and Dixon, 1966). Young seedlings are very sensitive to injury by frost heaving or drying winter winds. If not protected by a covering of snow or adequate windbreaks. nursery stock may be killed outright and transplants 10 to 15 years old may be killed or severely defoliated. On excellent sites in northern Idaho 120-year-old trees will average 175 feet in height and 22 inches in diameter (Wellner, 1962, Figs. 9 and 10). Dominant and codominant trees at age 80 in a well-stocked stand on an excellent site average about 132 feet tall and 17 inches in diameter making up a volume of about 77 thousand board feet per acre (Haig, 1932) (Fig. 11).

In the Cascade Mountains of Washington and Oregon, western white pine is also an important stand component but usually occurs in relatively small, scattered blocks rather than occurring over extensive areas as in northern Idaho. Trees in the Sierra Nevada Mountains of California grow at such high elevations that they are often deformed by wind and snow.

Western white pine is highly susceptible to the white pine blister rust disease (see Bingham[2]).

Pinus monticola has been crossed successfully with 6 other species of Subsection *Strobi* (Little and Righter, 1965; Wright, 1959) and putative hybrids have been obtained from crosses with 3 species of Subsection *Cembrae* (Bingham, Hoff, and Steinhoff, *in press*). Hybrid combinations involving *P. griffithii*, *P. strobus*, *Pinus peuce* Griseb., and *Pinus parviflora* Sieb. & Zucc. are being investigated at several stations throughout the world.



Figure 9. Mature western white pine stand 180 years old just prior to harvest--unmerchantable species already cut--Deception Creek Experimental Forest, north Idaho (U.S. Forest Service photo).



Figure 10. Stand of virgin western white pine near Pierce, Idaho (U.S. Forest Service photo).



Figure 11. A 65-year-old, thinned, western white pine stand, Deception Creek Experimental Forest (U.S. Forest Service photo).

DISCUSSION

Western North America has a variety of white pines with rather broad geographic ranges. It would seem, therefore, that most of these species would be adapted to quite a wide range of conditions but this is not necessarily so. Much of the variation which might be expected to accompany latitudinal displacement within species probably is offset by compensating elevational shifts. Climatic variables such as length of growing season and amount of annual precipitation are often quite similar, even between widely separated stands.

Several of the species grow on the same sites, especially near the extremes of their ranges. For example, western white pine and whitebark pine grow together in several areas as do whitebark and limber pines. Sugar pine and western white pine grow together in Oregon and California. Western white, whitebark, limber, and foxtail pines grow within a few yards of one another in the Sierra Nevada Mountains, and sugar pine grows only a few miles away.

SUMMARY

The foxtail pines comprise two species both of which grow in western North America. *Pinus balfouriana* is restricted to two areas in California while *P. aristata* is widely distributed. Neither species is commercially important but both have high esthetic value and may be useful for watershed protection or avalanche control.

There are six species of white pines native to western North America and Central America. All of them have wide geographic distributions. Three of the species, *P. ayacahuite*, *P. lambertiana*, and *P. monticola*, are commercially important; and a fourth, *P. strobiformis*, occurs mostly as scattered individuals and is harvested only on a small scale. The other two species, *P. albicaulis* and *P. flexilis*, are not often cut for timber but individual trees indicate that selection efforts could produce a more desirable tree if there were a demand for it.

There have been numerous efforts throughout the world to cross these six species with other white pines and many of the possible combinations have been completed. Several of the hybrid combinations show promise for a variety of uses and for planting areas not having native white pines. Further work using carefully selected parent trees should result in even more desirable hybrids intended for a specific use.

Planting programs for most of these species are now stopped in most areas awaiting the development of rust-resistant stock.

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FLOOR DISCUSSION

Discussion given here covers the previous paper by Dr. Kriebel. Moderator Bingham withheld discussion on the Kriebel paper so the two closely related papers could be considered at one time.

BINGHAM: The floor is open for discussion on the North and Central American white pines.

STEINHOFF: As a result of confusion over the taxonomic status of variety *chiapensis* of *Pinus strobus*, or *Pinus chiapensis*, Dr. Kriebel and I neglected to mention this variety or species in our oral presentation. However, it is covered by Dr. Kriebel in his formal paper. It is of rather limited distribution in Mexico, primarily restricted to tropical rain-forest conditions. I doubt that it would be useful to very many other people around the world who are working with white pines. On good sites it does attain considerable size. I have seen trees 2-1/2 to 3 feet in diameter, over 100 feet tall, but I don't know too much about its growth requirements.

DUFFIELD: Dr. Steinhoff, in a conversation this morning you mentioned a newly-discovered and newly-described pine from Mexico. Taxonomically it sounded as if it might belong in white pine Subsection *Balfourianae*. Will you comment?

STEINHOFF: At the outset I should caution that the proposed new Mexican pine species (*Pinus rzedowskii*) is only now being published by Xavier Madrigal and Miguel Caballero of the Section of Botany and Ecology, Department of Silviculture, of the Mexican National Institute for Forestry Research and of the Department of Statistics, National Forest Inventory, respectively, Mexico D.F. These authors very kindly loaned me a copy of their unpublished manuscript, complete with illustrative photographs, and I hesitate to preempt their rights by discussing it. However, because the presumably new species has great interest to persons at this session of the Advanced Study Institute who should be alerted to watch for publication, I'll presume to discuss it here. To answer Dr. Duffield's question, *P. rzedowskii* is both similar and dissimilar to the Subsection *Balfourianae* pines. Perhaps the most interesting point is its similarity to Section *Parrya* pines, especially to Subsections *Cembroides* and *Balfourianae* thereunder. Subsection *Balfourianae* pines (*P. balfouriana* and *P. aristata*), Subsection *Cembroides* pines (pinyon pines) of Section *Parrya*, as well as the new species, are all set apart

from the Section *Strobus* by having a dorsal rather than a terminal cone scale umbo. In the two *Balfourianae* species the umbo is armed with a sharp prickle, and in several of the *Cembroides* species (*P. cembroides* Zucc. and other pinyons, as well as *P. pinceana* Gord. and *P. nelsonii* Shaw), as well as the new species, the umbo is armed but only bluntly so. Also in the *Balfourianae* pines the seeds are definitely winged (as they are in the new species), while the *Cembroides* pines are wingless. Unlike the Section *Strobus* and Subsection *Balfourianae*, but like the *Cembroides* pines, the new species has fewer (3 to 4) than 5 needles per fascicle. I have suggested to Messrs. Madrigal and Caballero that the new species might be a bridging species, and that attempts at crossing it with Section *Strobus* and Subsection *Balfourianae* and *Cembroides* pines might be profitable from the taxonomic standpoint.[3]

VAN ARSDEL: I would like to suggest a slightly different interpretation on the outliers of *Pinus strobus* L. in the U.S., and particularly in the Mississippi River valley, than that suggested by Dr. Kriebel in his excellent paper. Dr. Kriebel suggested that the outliers were distributed according to microclimate. I'd like to suggest that the distribution could also be related to edaphic conditions--i.e., sandstone outcrops. In the upper Mississippi basin (above Tennessee) the northernmost outliers occur in Wisconsin on LaCrosse Sandstone, moving over into Indiana they occur on St. Peters Sandstone, further south in Indiana they occur on Manteyo Sandstone, and well to the south in Kentucky they occur on another massive sandstone outcrop. The point is that on these sandy outcrops there's no other tree competition. *P. strobus* occurs even on the warm, southwest-facing slopes where it gets pretty hot, rather than in cool, moist microclimates.

KRIEBEL: I believe that in Ohio there is a climatic factor involved, In that region we find *Pinus strobus* mainly restricted to stream valleys and rather protected sites that are definitely cooler than surrounding areas. However, I think what you say about edaphic (soil or geologic) factors in the upper Mississippi Valley may be quite true.

CALLAHAM: I have enjoyed this excellent geographic summary on the white pines, but I hear repeated references to crossability. I'm wondering if there is any intention to bring all of this evidence on crossability together. It would complete the proceedings for these panels if we could have some sort of crossability summary.

BINGHAM: Earlier this morning when I could see this crossability, and taxonomical questions arising, I asked Mr. Morton of my staff to circulate a handout--on white pine taxonomy and crossability--prepared for use with my own paper on taxonomy, crossability, and blister rust resistance to be given later this afternoon (Bingham, these proceedings). Apparently Mr. Morton was unable to complete the circulation due to the starting of this afternoon's session, but he'll finish the job now. The right, or last column of the handout on taxonomy, synonomy, botanical range, and crossability of 5-needled white pines summarizes present information on crossability amongst Subsection *Cembrae, Strobi,* and *Balfourianae* white pines.

[3] *Editors' note: Since this discussion it has come to our attention that Madrigal and Caballero have already published their proposed new species* Pinus rzedowskii--*see Madrigal, X. and M. Caballero. 1969. Una nueva especie Mexicana de* Pinus. *Inst. Nac. de Invest. Forestales Mexico. Bol. Tecn. 26, 12 p.*

STEINHOFF: Crossability of *P. monticola* was shortened to some extent in my paper because it has been covered extensively in a forthcoming paper[1] on genetics of western white pine.

DUFFIELD: There were several not too impressive slides shown of interspecies hybrids involving *Pinus monticola*. I'd like to point out, however, that *P. monticola* is a pretty good parent, better than some of the slides indicated. Many of the slides involved hybrids made at the Institute of Forest Genetics in Placerville, California, and the *P. monticola* parents used there came from high elevations in the Sierra Nevada Mountains. I wouldn't say these trees were alpine dwarfs, but relative to northern Idaho or other northwestern U.S. *P. monticola*, they are slow-growing. We checked this at Placerville in 1949, finding that *P. monticola* x *P. strobus* (or reciprocal) hybrids with the Sierra Nevada *P. monticola* parent were much slower growing than those with the Idaho parent. I think this would also apply to the other interspecies hybrids involving *P. monticola;* most of them were made using the slow-growing Sierra Nevada seed parent.

BINGHAM: I would add to that remark by saying that in 1953 or 1954, Dr. A. E. Squillace, then with my Experiment Station, planted trees of several Sierra Nevada *P. monticola* x *P. strobus* hybrids (with some Sierra Nevada *P. monticola* controls) at a location near Saltese in northwestern Montana. Performance of the Sierra Nevada hybrids and *P. monticola* controls was poor, compared to other nearby northern Idaho plantings of hybrids and controls with northern Idaho *P. monticola* parents. I shouldn't say too much here because different planting sites were involved.

KRIEBEL: I would suggest that because Dr. Heimburger has a tremendous knowledge about many of these white pines, especially *Pinus peuce*, he be called upon to comment on these white pine species and hybrids.

HEIMBURGER: We try to collect all the possible material in arboreta in the form of grafts. We have been interested in *Pinus peuce* Grisb. because of all the exotic white pines in Canada it grows farthest to the north--successfully so farther north than *P. monticola* or *P. griffithii* McClell. *Pinus peuce* also has been found to be resistant to the white pine weevil *Pissodes strobi*, as well as moderately resistant to white pine blister rust. Later this afternoon in my paper on blister rust resistance tests in eastern North America (see Heimburger, these proceedings), I will show some photographs and data on its resistance to blister rust. This species is, of course, in itself rather useless, because it grows too slow. But it has good form, good branching habit. Also, its hybrids, particulary with *P. monticola* and *P. griffithii*, and to a lesser extent with *P. strobus*, are very good. I will also cover its precocious flowering this afternoon.

[1] *Editor's note: The paper referred to, one of a series on genetics of North American trees fostered by the Society of American Foresters and published by the U.S. Forest Service, is: Bingham, R. T., R. J. Hoff, and R. J. Steinhoff. Genetics of western white pine. It will probably be published in 1971 as one of a series of Forest Service, Washington, D.C., Office Research Papers.*

RELATIVE BLISTER RUST RESISTANCE OF NATIVE AND INTRODUCED WHITE PINE SPECIES IN EUROPE

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ABSTRACT

Native European white pines, and those introduced from Asia and North America are considered in three groups. Native European white pines include *Pinus cembra*, *P. sibirica* (possibly one of the original hosts of white pine blister rust, *Cronartium ribicola*), and *P. peuce*. *P. cembra* and *P. sibirica* seem to be moderately to highly resistant under natural exposure to the rust in the Italian and Swiss Alps, in Germany, Denmark, Belgium, Finland, France, Great Britain, Norway, Poland, and Sweden. Occurrence of the rust in natural stands of *P. peuce* is little known, but under introduction into more northerly European localities it is seen to range from almost as susceptible as *P. strobus*, to highly resistant. Performance of hybrid seedlings from Danish crosses between *P. peuce* and *P. strobus* has demonstrated the ability of *P. peuce* to transmit its resistance to offspring. Often the hybrid seedlings were heavily infected, but--unlike *P. strobus* seedlings--they survived.

Asiatic introductions include *P. armandii*, showing a high degree of resistance; *P. griffithii* (syn. *P. wallichiana*), ranging from moderately to highly resistant; *P. koraiensis*, found to be moderately to highly resistant in both Europe and North America, and *P. parviflora*, resistance of which is largely unknown.

North American white pine introductions include *P. albicaulis* (rare but always heavily attacked), *P. flexilis* (generally found highly susceptible), *P. strobus* (moderately to highly susceptible), *P. lambertiana* (more susceptible than *P. strobus*), and *P. monticola* (fairly rare but always highly susceptible).

Emphasis is given to the need for further investigation of variation in resistance within white pine species--especially *P. armandii*, *P. peuce*, *P. griffithii*, *P. cembra*, and *P. sibirica*. To make full, yet judicious and economical use of resistant germ plasm now, or soon available, international cooperation will be a necessity.

INTRODUCTION

Pinus strobus L. was the most important of the 11 native and introduced 5-needled pine species tried in Europe. From its introduction early in the 17th century until blister rust stopped it in the late 1800's, this tree was valuable for European conditions. My purpose here is to evaluate this tree and each of the 10 other native and introduced species for their resistance to attack by the fungus *Cronartium ribicola* J.C. Fisch. ex Rabenh. The species will be divided into three groups: Native white pines (European white pines); white pines introduced from Asia; and white pines introduced from North America.

NATIVE WHITE PINES (EUROPEAN WHITE PINES)

PINUS CEMBRA L.

Pinus cembra was the original host for *C. ribicola*, which was discovered in 1854 by Dietrich (1856) in Estonia on *Ribes nigrum* L. and other *Ribes* species, and also on *Pinus strobus*. He named the fungus *C. ribicola* without any description. In 1872, J. C. Fischer made a short description of the fungus also using the name *C. ribicola*. Klebahn (1888) was the first to show the identification between *Peridermium strobi* Kleb. and *C. ribicola*. *P. cembra* is attacked in its native area in high elevations in the Alps and the Carpathian Mountains. *Pinus sibirica* Du Tour is attacked in its native area in western and central Siberia to northern Mongolia with isolated occurrences on the Kola Peninsula. The attack often is not conspicuous as the tree possesses a high degree of resistance. In the Piedmont Alps in Italy with *R. alpinum* L. nearby, all the trees were attacked; but these were only branch infections, so some sort of resistance apparently was present. No trees were killed (Gremmen, *personal communication*). In the Botanical Garden in Hann. Münden, the attack on *P. cembra* was small as compared with *P. strobus*, *P. lambertiana* Dougl., *P. flexilis* James, *P. monticola* Dougl., and *P. cembroides* Zucc., whereas *P. strobus* x *P. griffithii* McClell. (*P. griffithii* McClell is synonymous with *P. wallichiana* A.B. Jacks.), *P. peuce* Griseb. and *P. griffithii* were not infected (Meyer, 1954). In Denmark in the Forest Botanical Garden, *P. cembra* has been grown since about 1890 and no infections have been observed. It is also recorded in Belgium, Finland, France, Great Britain, Norway, Poland, and Sweden (Buchanan, 1964).

PINUS PEUCE

Native to Albania, Yugoslavia, Bulgaria, and northern Greece, *P. peuce* possesses a high degree of resistance although it can be attacked by the fungus. *P. peuce* was infected to the same extent as *P. strobus* in an experimental area in Schleswig-Holstein (Schenck, 1939). Crosses with *P. strobus* (S.873-45) made in Denmark in 1945 show that *P. peuce* transfers its resistance quality to its offspring. Open pollinated (S.874-45) offspring of the hybrid *P. strobus* x *P. peuce* shows the same tendency. The graphs in Fig. 1 through 4 illustrate the mode of resistance that is transferred to the offsprings. Figures 1 and 2 show the course of infection for 16 years from two seed collections of *P. strobus* (S.867-45 and S.863-45). No individuals are alive after 16 years.

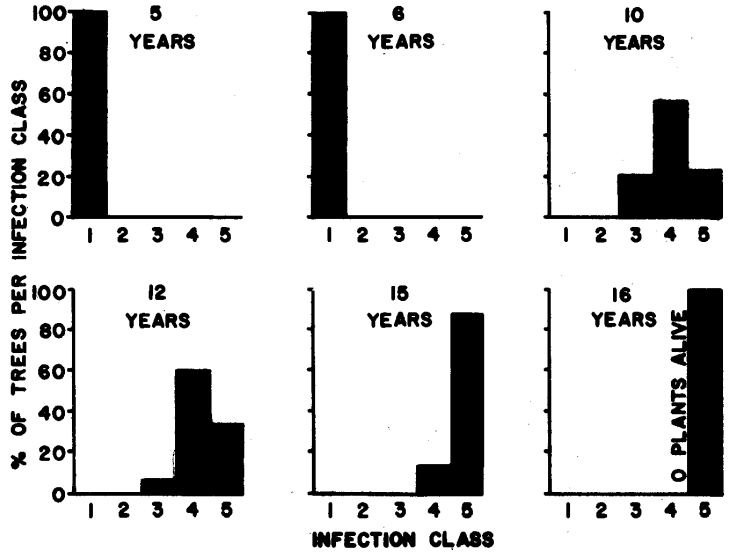


Figure 1. Degrees of infection of seedlings of *Pinus strobus* at various ages by *Cronartium ribicola*: seed collection S.867-45. Infection classes: 1--healthy (not infected), 2--healthy (previous infections were defeated), 3--branch infection only, 4--stem infections, 5--dead.

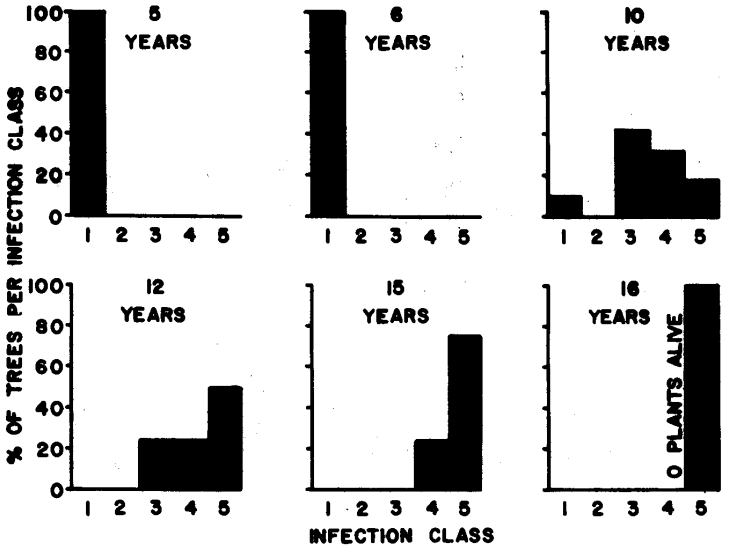


Figure 2. Degrees of infection of seedlings of *Pinus strobus* at various ages by *Cronartium ribicola*: seed collection S.863-45. Infection classes: 1--healthy (not infected), 2--healthy (previous infections were defeated), 3--branch infection only, 4--stem infections, 5--dead.

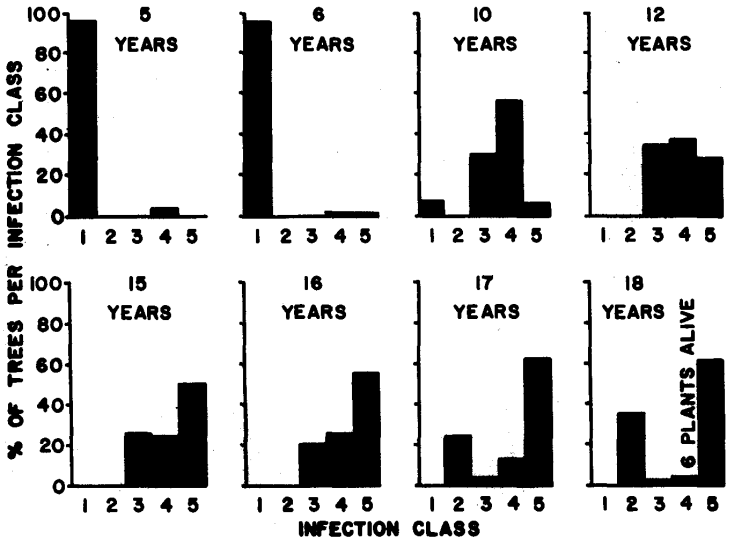


Figure 3. Degrees of infection of hybrid seedlings of *Pinus strobus* x *Pinus peuce* at various ages by *Cronartium ribicola*: seed collection S.873-45. Infection classes: 1--healthy (not infected), 2--healthy (previous infections were defeated), 3--branch infection only, 4--stem infections, 5--dead.

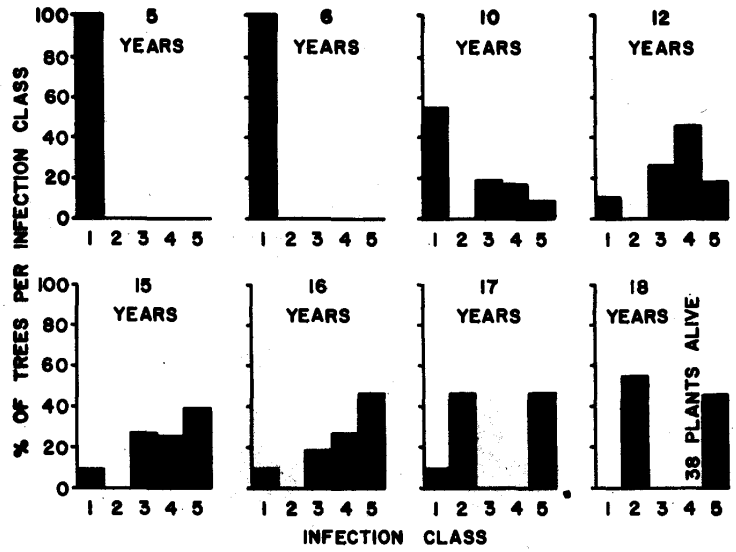


Figure 4. Degrees of infection of open pollinated seedlings of a hybrid between *Pinus peuce* x *Pinus strobus* at various ages by *Cronartium ribicola*: Infection classes: 1--healthy (not infected), 2--healthy (previous infections were defeated), 3--branch infection only; 4--stem infections, 5--dead.

Figure 3 shows the infection results of the cross *P. strobus* x *P. peuce*; many of these offspring survived. The infection level is high, nearly as high as on the *P. strobus* offspring, but the plants were seldom killed. Figure 4 shows an offspring from open pollination of a cross (*P. strobus* x *P. peuce*). The course of the attack is very similar to that seen in Fig. 3.

In 1958, Denmark foresters harvested seed from selected trees in the natural range in Yugoslavia. No infections have been recorded in the progenies. In England, 1 of 22 individuals was infected in a test (British Forestry Commission, 1960). In Germany, *P. peuce* has not been infected in the Botanical Garden in Hann. Münden, in the arboretum at Hørsholm, nor in the Forest Botanical Garden since 1876.

INTRODUCED WHITE PINES FROM ASIA

PINUS ARMANDII FRANCH.

This species is native to western and southwestern China, southeastern Tibet, northern Burma, and northeastern India, and to the islands of Hainan and Taiwan. The first generation in Denmark was not attacked by *C. ribicola*. *P. armandii* was introduced into Denmark in 1926; seed was collected by Joseph F. Rock, October 1925, in central Kansu. After open pollination (1957), offspring from the first generation, exposed to natural infection, did not show any attack by *C. ribicola* although there was high infection of *P. strobus* seedlings in the same area.

PINUS GRIFFITHII

This species is native to the Himalaya Mountains, West Pakistan, northern Burma, and Yunnan province, China. It is supposed to be resistant to *C. ribicola*. Meyer (1954) mentions a hybrid (*P. strobus* x *P. griffithii*) that was not infected by the fungus. Schenck (1939) refers to an attack on the species in Oldenburg, Germany. The Report on Forest Research (British Forestry Commission, 1961) mentions that *P. griffithii* again was noticeably resistant and *P. holfordiana* A.B. Jacks. (*P. griffithii* x *P. ayacahuite* Ehrenb.) was susceptible. Boyce (1926) mentioned findings near Oxford, England, where *P. strobus* was heavily infected and *P. griffithii* was not. In the Arboretum at Hørsholm a hybrid between *P. griffithii* and *P. strobus* was infected, whereas the pure *P. griffithii* was healthy. The rust was also recorded in Belgium, Sweden, and Switzerland (Spaudling, 1929).

PINUS KORAIENSIS SIEB. & ZUCC.

This species is native to Korea, eastern Manchuria, southeastern Siberia, and Japan. Schenck (1939) states that *P. koraiensis* is not attacked by *C. ribicola* in the U.S.A., and that *P. koraiensis* in Germany situated near a highly infected stand of *P. strobus* was not attacked.

Pinus koraiensis in Denmark, grown in the Forest Botanical Garden since 1890, has not been attacked by *C. ribicola*, and the same is the case with several offspring from these trees.

PINUS PARVIFLORA SIEB. AND ZUCC.

This species is native to Japan and the Korean island Utsuryo. It is known in Europe as an ornamental tree and is common in many botanical gardens outside its natural range. Its resistance to attack by *C. ribicola* has not been investigated in Europe. Schenck (1939) mentions the same level of resistance as shown by *P. peuce*. The species has been grown since 1889 in Denmark without showing attack by *C. ribicola*.

INTRODUCED WHITE PINES FROM NORTH AMERICA

PINUS ALBICAULIS ENGELM.

This species is native to western Canada, British Columbia, western U.S.A., Washington, Oregon, California, Idaho, Nevada, Montana, and Wyoming, at high elevations. It is highly susceptible to *C. ribicola* and is seen very seldom in Europe, even in botanical gardens.

PINUS FLEXILIS

This species is native to western Canada and U.S.A., Rocky Mountains from southern Alberta and British Columbia to northern New Mexico. In Europe it is not found outside the botanical gardens. It is highly susceptible to attack by *C. ribicola*. Eighteen trees in the Arboretum were heavily attacked and some were killed. In Norway (Jørstad, 1949), *P. flexilis* is heavily attacked; however, in 1923, its susceptibility was reported to be about equal to *P. cembra*. And a record from Lithuania in 1937 reports an attack on *P. flexilis* in the Kaunas Botanical Garden, where a series of experiments was carried out from 1935 to 1938.

PINUS LAMBERTIANA

This species is native to western U.S.A. in the Coast Range and the Sierra Nevada. It is, according to Schenck (1939), as susceptible as *P. strobus*. A stand in Weinheim in Berckheimschen seemed to be more damaged than *P. strobus*, which means that it was nearly as susceptible as *P. monticola*.

PINUS MONTICOLA

This species is native to western canada and U.S.A., from southern British Columbia to northern Idaho, northwestern Montana, and eastern Oregon and south through the Cascade Mountains of western Washington and Oregon to the southern end of Sierra Nevada in California. *P. monticola* is as susceptible to *C. ribicola* as *P. flexilis* and *P. albicaulis*. *Pinus monticola* has been tried in different European countries, mostly in parks and botanical gardens. Hahn (1929) reports heavy attacks on *P. strobus* and *P. monticola* in Scotland. In Denmark, in the Forest Botanical Garden and in the Arboretum since 1937, *P. monticola* is still alive although infected.

PINUS STROBUS

This species will be covered in depth by Mr. Gremmen, in the paper that follows.

CONCLUSION

Pinus armandii, P. peuce, P. griffithii and to some extent *P. cembra* seem to possess different degrees of resistance against attack by *C. ribicola.* Little has been done to investigate the variation of resistance within species. In some cases this is because it is difficult to go into the natural distribution area; in other instances it is impossible to overcome the economical barrier connected with such a project. This investigation will be made when necessity demands it. Therefore we have to face the problems now, to plan the procedure and distribute the tasks to be carried out by relevant people and countries.

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FLOOR DISCUSSION

Panel leader Bingham withheld discussion of this paper until after two other closely related papers, one by Gremmen, the other by Bakshi, had been given. The discussion will be found following the Bakshi paper.

RELATIVE BLISTER RUST RESISTANCE OF *PINUS STROBUS* IN SOME PARTS OF EUROPE

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ABSTRACT

The last 40 years of European work on resistance to the white pine blister rust disease (pathogen *Cronartium ribicola*) is reviewed. Dutch experimental work testing resistance of various *Pinus strobus* provenances and a few seedling progenies from crosses among phenotypically resistant *P. strobus* selections has been disappointing. Neither resistant provenances nor individual trees have been observed. Work is continuing with more carefully selected test materials. Some German workers have reported "resistant biotypes" and "resistant provenances," while others have shared the Dutch experiences of failing to find resistance in seedlings of crosses among phenotypically resistant *P. strobus* parents. Infection of susceptible root-stocks has caused problems in interpreting results of some experiments. Some observations on "natural resistance" of *P. strobus* in Europe are unexplained. They may be the result of environmental conditions inhibiting development of the pathogen. More work on physiological races of *C. ribicola* is needed. The foundation of disease gardens outside North America, wherein various races of the rust can be brought together with potentially resistant white pine materials and the association studies in detail, is strongly advocated.

INTRODUCTION

In our mind we go back to 1927, the year when eastern white pine (*Pinus strobus* L.) got a first class funeral at a German forestry meeting in Frankfurt/Main. The tree succumbed as a result of blister rust attack (pathogen *Cronartium ribicola* J.C. Fisch. ex Rabenh.). The funeral sermon was delivered by Professor C. von Tubeuf, the well-known plant pathologist. Nevertheless, in 1934 the coffin was reopened by Dr. Wappes at a forestry meeting in Bonn, and what appeared? Although buried at Frankfurt the tree was still alive. One year later rehabilitation followed at a Würzberg meeting and replanting of the tree in the "middle of the German forest" was authorized.

Since 1939, Dr. H. van Vloten had pleaded for this beautiful and valuable forest tree in The Netherlands, arguing, "Must we abandon the introduction of exotic trees in our forests because of certain diseases? No, as little as we like to do without our potato from South America, or our cereals and fruit trees from elsewhere in the world " (author's translation).

DUTCH RESEARCH

To support his words van Vloten (1939) started research on blister rust, looking for resistant *P. strobus* trees to promote their further use in Dutch forests. As a result of his work, he advised foresters to avoid the use of *P. strobus* seedlings originating from commercial nurseries and, instead, to raise their own plants in the forest by sowing.

His experiments with eastern white pine and blister rust were demonstrated at the September 1939 meeting of the Dutch Forestry Society.

In 1941, 24,000 plants, exposed to blister rust in the nursery and representing 43 different provenances, were transferred to the Loenermark Forest. Provisional observations already indicated that all provenances were seriously infected. A difference in the development of the aecidia (0 to 72%) was noticed in these 3-year-old plants, but van Vloten (1941) avoided a definite stand regarding possible resistance.

After the foundation of the Forest Research Station at Wageningen, of which Dr. van Vloten became Director, work on this theme was continued by the present author under the Director's guidance. For this purpose, 9 different lots of *P. strobus* seed--4 from surviving trees in long-exposed Canadian, Dutch, and Austrian plantations, and 5 from controlled crosses between pairs of phenotypically resistant North American trees found by A. J. Riker and his associates at the University of Wisconsin, the Lake States region of the U.S.A.--were obtained and tested from 1952 to 1961. Identity of the 9 lots is shown in Table 1.

Seed lots were sown in a nursery at the Forest Research Station, "De Dorschkamp", in both 1952 and 1953. Then, at the start of their second growing season, seedlings were transplanted into two rectangular experimental plots. The first plot, containing all 9 sources, was established in 1953; the second plot, with 7 of the 9 sources, was established in 1954. Some seed source lots were larger and produced more seedlings than others. Regardless of size, the seedling lots were divided into basic replicates of 10+ seedlings. Replicates per seedling source varied from 2 to 12 in the plot established in 1953, from 1 to 28 in the plot established in 1954 (Table 1). There were 52 row-plot replicates of 10+ seedlings each in the 1953 plot, 60 in the 1954 plot. These were assigned random positions and then planted in two rectangular plots. Rows of trees alternated with rows of black currants (*Ribes nigrum* L.), leaves of which were inoculated with aeciospores of *C. ribicola* in the early summer prior to the autumn pine infection periods.

Test seedlings were carefully examined each year after their initial exposure to *C. ribicola* infection. Noted were those plants showing suspicious rust-like symptoms, those with definite early symptoms of the rust disease, those developing aecia, and those killed by the rust disease. Percentages of seedlings in the 9 seed lots killed by the rust through 1959 are shown in Table 1. By 1961, all seedlings had been killed by the rust and the experiment was terminated.

Our major conclusions were as follows: (1) No genuine resistance was observed in any of the 9 *P. strobus* sources investigated; (2) a slight difference in degree of attack between individual seedlings was noticed, some of the more lightly attacked seedlings being characterized by the absence of older needles. According to Spaulding (1925), reduced retention of needles may be the means by which plants escape branch infection.

Table 1. Performance of seedlings from 9 *Pinus strobus* sources when exposed to white pine blister rust in 2 experimental plots at Wageningen, The Netherlands

Seed source		Percentage of seedlings killed by *C. ribicola*					
		1953 plot			1954 plot		
Our identifying number	Collector's source	No. replicates[a]	1957 insp.	1959 insp.	No. replicates	1958 insp.	1959 insp.[b]
52-02	Coll. 1950, Pointe Platon, Quebec plantation, C. Heimburger "strain 26"	12	25	87	12	20	30
52-14	Coll. 1948 and 1949 from Dutch plantation at Groesbeek	12	31	83	28	21	28
52-34	Austrian selection-stand plantation by W. von Wettstein	12	40	79	12	28	29
52-36	Coll. 1951 from controlled cross of Univ. Wisc. phenotypically resistant selections 6x9	3	73	96	2	20	25
52-37	Ditto, 36 x 38	2	No data	90	0	--	--
52-38	Ditto, 191[c] x 7	2	No data	93	0	--	--
52-39	Ditto, 192 x 5	3	43	93	3	20	23
52-40	Ditto, 312[c] x 38	3	70	100	2	60	65
52-41	Ditto, 314 x 18	3	50	87	1	30	40

[a] Each row-plot replicate contained at least 10 seedlings.

[b] In the 1959 inspection, seedlings on the 1954 plot had been exposed to rust 1 year less than those on the 1953 plot; lower levels of rust kill may also be associated with relatively poor conditions for rust infection in 1954.

[c] University of Wisconsin selection nos. 191 and 312 in Wisconsin have been found to be slightly above average in transmitting resistance to their progenies; i.e., 8 to 10% disease-free plants vs. 0 to 7% disease-free plants in progenies from other trees (personal communication from Dr. R. F. Patton, June 20, 1969).

Since these results were very disappointing, we hesitated to continue along these lines. Nevertheless, early in 1966 our Station commenced work in assembling a collection of white pine materials that were perhaps better identified in respect to their blister rust resistance. These materials were received as scions. They were grafted on 4-year-old, potted *P. strobus* rootstocks in spring 1966, and were transplanted to the nursery in 1967. They are now under observation by persons in two of our Forest Research Station Sections (Pathology and Resistance Research and Forest Genetics of Conifers) at Wageningen. New materials now under observation are outlined in Table 2.

OTHER EUROPEAN RESEARCH

The kind of work done by van Vloten (1939, 1941) was also tackled in Germany by several research workers.

Rohmeder (cf. Lehmann, 1950/1951) mentioned that about the year 1940 seed from *P. strobus* originating from various localities in North America, partly collected from single mother trees, had been received. The 2- and 3-year-old plants obtained from them were afterwards inoculated several times with *C. ribicola* spores and then transplanted in two different plots, one close to Nürnberg, the other near München. Some years later it appeared that none of these plants showed a "complete immunity", although differenes in resistance were observed. Some of these provenances showed a 2 to 4% loss by the rust, others up to 36% during the first 10 years of observation.

Again Rohmeder (1954) reported that in 1952 his Institute received "durchgezüchtetes blasenrostresistentes Strobensaatgut aus der gelenkten Kreuzung resistenter Pfropflinge" by courtesy of Dr. A. J. Riker and Professor Dr. R. F. Patton.

Dr. Patton informed me[1] that the seed sent to Dr. Rohmeder were progenies of *P. strobus* selections that had proved to be resistant, to varying degrees, by their responses to both artificial and natural inoculations. The following progenies, to be called phenotypically resistant, were sent: Nos. 36 x 38; 191 x 38; 312 x 38; 312 x 129, and 314 x 18. Nos. 18, 36, 129 and 312 were rated as highly resistant; 38, 191 and 314 as having a moderate degree of resistance.

Rohmeder stated later[2] that these seedlings were exposed to a severe, natural infection as well as to artificial inoculation by means of spores of the *Cronartium* fungus in the Experimental Garden at Grafrath. Later on it appeared that all plants became heavily infected by the rust and consequently the experiment was terminated.

It is interesting to note that three of these progenies (36 x 38, 312 x 38, and 314 x 18) suffered a similar fate at Wageningen.

In spring 1960, Rohmeder[2] received a number of scions originating from 8 resistant *P. strobus* trees through the intermediary of Drs. Riker and Patton. After successful grafting at Grafrath, the whole plot was exposed to artificial and natural infection, the rust spreading from

[1] *Personal communication, June 20, 1969.*
[2] *Personal communication, February 13, 1969.*

Table 2. Blister rust resistant white pine materials grafted in 1966 and now under observation at Wageningen, The Netherlands

Species or interspecies hybrid	Cooperator and his identifying selection numbers	Cooperator's remarks on source and resistance of material
Pinus strobus	R. F. Patton, Univ. Wisconsin selection nos. 18,30,312,327 & 343	"Resistant selections which seem better than average resistance transmitters"
	C. Heimburger, Ontario Dept. Lands & Forests selection nos. 46,145,333,459,507,508,519, 535,554,568,572,615 & 644	No. 46 Cherokee, N.C.; 145 from Pointe Platon, Que., resistant tree; 459,507,508,519,535,615, and 644 F_1's from crosses of resistant Pointe Platon trees; 554 and 568, wind pollinated F_1's from resistant Wisconsin trees; 333 a "survivor" at Indian Head Nursery, Sask.; 572 Angus, Ont., resistant tree.
P. griffithii McClell. x *P. strobus*	C. Heimburger, Ont. Dept. Lands & Forests selection nos. 826,920,923,927 & 931	*P. griffithii* (Arnold Arboretum x Wind) x Ont. Dept. Lands & Forests 322
P. strobus x *P. griffithii*	Same cooperator and station, selection nos. 295 & 772	295 K. Sax Arnold Arb. hybrid; 772 Ont. Dept. Lands & Forests *P. strobus* ♀ x Institute of Forest Genetics, Placerville, Calif. (Lucknow, India, origin) *P. griffithii* .
P. parviflora Sieb. & Zucc. x *P. strobus*	Same cooperator and station, selection no. 293	293 K. Sax Arnold Arb. hybrid.
P. strobus x *P. parviflora*	Same cooperator and station, selection no. 319	319 Hunnewell Estate, Wellesely, Mass., natural hybrid, direction of cross unknown
P. monticola x *P. strobus*	R.T. Bingham, U.S. Dep. Agr., Forest Serv., Intermountain Forest & Range Expt. Sta., individual F_1 hybrids 19x*P.st.* 13-no. 1, 19x *P.st.* 22-no. 2, and 63x*P.st.* 15-no. 1	"Hybrid seedlings were artificially inoculated 2 to 3 times at ages 1 to 6, exposed to natural infection from planted *Ribes* spp. from age 3 to 4 and up to age 6 yrs; yet survived." *P.st.* 13 = Univ.Wisc. 19, *P.st.* 15 = Univ.Wisc. 30

planted *R. nigrum* L. During the first 5 years all grafted trees remained healthy, but since 1968 some plants have been observed to be attacked by the blister rust fungus.

Professor Patton[1] informed me that the scions sent to Dr. Rohmeder in 1960 were of the following selections: 1, 6, 30, 36, 191, 312, 327, 343, 353, and a susceptible control C-6. All of these are resistant selections, but 191 might be classed as moderately resistant. Selection 1 seemed to be highly resistant, but no information exists on its resistance-transmitting ability. No. 327 so far has given the most promise of ability to transmit resistance to its progeny.

Liese (1936),when describing the attack of *Peridermium pini* (Pers.) Lev. on *Pinus silvestris* L. stated that "in my opinion, the natural tendency for the attack by *Peridermium pini* is heritable" (my translation). Moreover, he believed this to be the same with regard to *C. ribicola* in *P. strobus*, referring to some observations done by Eriksson (1896). Eriksson raised eastern white pine plants in 2 different garden beds with only 20 meter interspace. In one bed, a 90 to 95% attack had been observed in a 7- to 8-year period, whereas not a single trace of rust was observed in the other bed.

Lehmann (1950/1951, citing a personal communication of January 2, 1950, from Liese) mentioned that before World War II extensive research with regard to possible resistance in eastern white pine against blister rust was carried out at Eberswalde (Germany). Seed from 25 various *P. strobus* provenances originating from natural localities of this tree in the United States have been obtained. Liese stated that "it has been demonstrated that all provenances contained susceptible as well as resistant biotypes" (my translation).

Scholz (1960) assessed a *P. strobus* trial originally founded by Professor J. Liese and Professor C. A. Schenck in 1938 in the Forest Range Chorin near Eberswalde. This trial was non-replicated with some sources having as low as 3, but up to 198 seedlings. It consisted of 10 German and 26 American provenances, originating from seed. During 1955 and 1956 the remaining trees were checked by Scholz on the presence of the aecidial stage of the fungus. He observed a difference in attack between the provenances, and within each provenance between the progenies, varying from 6.8 to 23.1%. From a total of 56 progenies (36 provenances), 13 progenies remained free from the disease, among them 1 provenance comprising 3 progenies from Tennessee (Emory River). Scholz informed me[3] that provenance 7 a-c (Tennessee, Emory River) is still *without* attack.

Scholz (1960) also mentioned another experiment dealing with research on resistance in *Pinus strobus* started in 1954. For this trial 422 grafts from 27 selected trees and 800 4-year-old nursery transplants were used. *R. nigrum* and *R. sanguineum* Pursh. bushes were interplanted. In 1956 the first symptoms of blister rust were observed in both grafted plants and seedlings. Many of them showed the aecidial stage. In 1957 nearly all *P. strobus* palnts were infected by the rust. In 1958 all grafted plants, with the exception of one clone, were heavily infected or even killed. Of the 800 plants all died except two plants.

[3] *Personal communication, May 5, 1969.*

Scholz (1960) stated that in fact a number of grafted plants had died as the result of attack of the rootstock by *C. ribicola*.

Scholz (1960) also reported on wound inoculations with aecidiospores executed in June 1954, the spore material originating from three different localities, Chorin, Colbitz and Waldsieversdorf. In February 1956 a considerable amount of "old aecidia" were noticed. However, it is important to mention that Scholz himself is not quite sure whether the results were due to his inoculations or to "Fremdinfektionen". Boyer (1964) subsequently has reported his failure to secure inoculation of *P. strobus* by viable aeciospores, with or without wounding.

Meyer (1954) reported on 32 healthy *P. strobus* of about 40 years age selected in the Odenwald Forest. These trees were carefully checked for the presence of the rust by examination of the crown and side branches. Scions were taken from these "healthy" trees in 1950/1951. By spring 1954, it was demonstrated that 4 clones were susceptible to the rust, whereas 2 other clones seemed suspicious. Meyer believes that, in the near future, many more clones will prove to be non-resistant.

In Denmark *P. strobus* and crosses between *P. strobus* and *P. peuce* Griseb. were tested for resistance to blister rust. The results of this work will be reported in a separate paper to be given at this symposium by Dr. B. Søegaard.

Now and then incidental observations with regard to "resistance" in older stands of eastern white pine have been made in various parts of Europe. Schwend (1949), for example, reported on the occurrence of healthy *P. strobus* stands in the environs of Kraków (Sanok and Lesko), a region from which the pathogen is well-known.

DISCUSSION

In view of further work to be done with regard to resistance research in eastern white pine against the blister rust fungus, particularly when applying grafting techniques, I would like to draw attention to the importance of healthy rootstocks. When using rootstocks from unknown origin, a risk is taken that these already may be infected by the rust; subsequently this may cause considerable confusion when estimating the degree of resistance of the grafts, since infection of the rootstock may lead to a die-back of the whole plant. Therefore rust-free rootstocks are of basic importance.

Another problem in developing resistant white pines is our present lack of knowledge on the existence of physiological races of the fungus. Much more detailed information on this subject is needed to supplement the scanty information given by Anderson and French (1955).

In comparison with the abundant information on *Melampsora* rusts of poplars (van Vloten, 1949), data on possible races in the fungus *C. ribicola* are just becoming available (see Hoff and McDonald, these proceedings).

Further research by inoculation of *Ribes* spp. leaves by various rust provenances might be helpful in this work, using the leaf disc method in petri-dishes developed during study of the *Marssonina* leaf blotch disease in poplar (Gremmen, 1964). Moreoever, we need to study the

reaction of these rust provenances on eastern white pine itself, a work not so easy to accomplish.

Since *C. ribicola* is a native fungus of Eurasia, possibly originally inhibiting *Pinus cembra* L., it would not be surprising at all that only a restricted number of strains of the fungus entered North America. If so, newly developed resistant trees on the American continent might afterwards prove to be susceptible to other strains of the pathogen still existing in Eurasia. However, there seems to be disagreement about whether *P. cembra* of the Alps is the original host, and the Alps the gene-center for *C. ribicola* (Spaulding, 1929). Other species, notably *P. sibirica* Du Tour, *P. griffithii*, *P. armandii* Franch., and *P. koraiensis* Sieb. & Zucc. are also highly resistant, and their ranges are also likely gene-centers (see Bingham, first of two papers in these proceedings).

For this reason further work on this theme should be encouraged under European and Asiatic conditions; in fact such work appears to be an absolute necessity in order to make progress in this field. The foundation of two or more disease gardens is needed. Here various rust provenances and resistant host plants that have been only tested locally can be brought together and studied in detail.

Since these aspects can only be solved by more intensive international cooperation, these problems will be faced in the new Subcommittee on "International Resistance Test Facilities" forming part of the IUFRO Blister Rust Committee of the Working Group on Genetic Resistance to Forest Diseases and Insects. The target of this Subcommittee is to contribute to a further solution of these details in the blister rust resistance problem. If the rust race problem can be probed, and solved with the help of such test facilities, then utility of resistant varieties of North American white pines will be greatly enhanced there, and new perspectives will be opened for replanting these valuable species in Europe and Asia.

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FLOOR DISCUSSION

Discussion of this paper was withheld until all 3 papers in the panel on "Relative Blister Rust Resistance of Native and Introduced White Pines of Europe and Asia" were completed. It will be found following the last paper in the panel, by Dr. B. K. Bakshi.

RELATIVE BLISTER RUST RESISTANCE OF NATIVE AND INTRODUCED WHITE PINES IN ASIA

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ABSTRACT

Relative white pine blister rust resistance of six Asian 5-needle pines (*Pinus armandii, P. sibirica, P. pumila, P. wallichiana* (synonym *P. griffithii*), *P. koraiensis* and *P. parviflora*) in indigenous locations, and also of *P. strobus* and *P. ayacahuite* introduced in Asia is discussed. Of these, *P. wallichiana, P. koraiensis* and *P. sibirica* are attacked by the blister rust but are fairly resistant, and the remaining species have not been found to be reported as attacked by the rust in Asia. A rust reported to be *Cronartium ribicola* has been reported but not verified in Japan; *C. ribicola* is definitely present in South Korea both on *Ribes* and *P. koraiensis*, if at different localities on each of these hosts.

Peridermium indicum, the aecial stage of *C. ribicola* on *Pinus wallichiana*, is, at least morphologically, distinct from *Peridermium strobi*, the aecial stage of the rust on *Pinus strobus*.

Intensive surveys, critical morphological study of *C. ribicola* based on the material collected all over the world, and cross inoculation experiments are suggested to determine the bearing of biological phenomena (especially racial diversity and possible autoecism) in *C. ribicola* on the relative blister rust resistance of 5-needle white pines.

INTRODUCTION

Of the almost 20 species of white pines in the world, 15 are important as forest and timber trees. Five of these--*Pinus armandii* Franch., *P. sibirica* Du Tour, *P. wallichiana* A. B. Jackson (syn. *P. griffithii* McClell.). *P. koraiensis* Sieb. & Zucc. and *P. parviflora* Sieb. & Zucc.--are indigenous to Asia. *P. pumila* Regel is also very widespread, if not a timber species, in eastern Asia. Relative resistance of these indigenous Asian pines to white pine blister rust (pathogen *Cronartium ribicola* J. C. Fisch. ex Rabenh.), and also susceptibility of other white pines introduced in Asia are discussed below.

NATIVE ASIAN WHITE PINES

PINUS ARMANDII

Indigenous in central China, Burma, Taiwan, Hainan Tao, and in North East Frontier Agency, India.

This species is known to be highly resistant to blister rust infection in its native home and also where introduced into Canada, France, and United States (Buchanan, 1964). *P. armandii* has been successfully inoculated with *C. ribicola* in the U.S. (Bingham, these proceedings).

PINUS SIBIRICA

Indigenous in the U.S.S.R. (Central Siberia, N. China, and North Mongolia.

The blister rust is recorded on this pine in Russia, and it appears to be moderately susceptible in the U.S.S.R. (Spaudling, 1929).

PINUS PUMILA

Indigenous in northwestern Asia, extending north almost to the Arctic Ocean, east to the Bering Sea, west to northern Mongolia and Lake Baikal, south to Korea and Central Honshu, Japan.

P. pumila appears to be moderately resistant (Spaulding, 1929), and *C. ribicola* appears to be absent on it in Korea.[1]

PINUS WALLICHIANA

Indigenous in temperate regions throughout the Himalayas from Afghanistan to north Burma. *C. ribicola* is recorded on this pine in western Himalayas only, though sporadically. Forty-year-old sample stock of *P. wallichiana* in Korea has remained free from infection of blister rust.[1] The species was found to be resistant in different locations in Europe where *Pinus strobus* was attacked (Spaulding, 1929), and although it was artificially inoculated it proved to be fairly resistant in North America (Bingham, 1967; Heimburger, 1962).

PINUS KORAIENSIS

Indigenous in north eastern Asia from south Siberia through Manchuria to Korea and central Japan.

This species is attacked by *C. ribicola* in Korea. Dr. S. K. Hyun[1] reports that there was a record of blister rust infection in 1936 in an 8-year-old plantation of this pine in Kyunggido Province, Korea, but no significant damage on the host was observed. In 1967 the rust was reported from Kangwondo Province, Korea, in 60 ha of 7 to 11-year-old plantations. About 60 percent of the trees were infected and 30 percent were severely damaged, resulting in a few dead trees. However, *Ribes*

[1]*Dr. S. K. Hyun, personal communication, 1969.*

appears to be absent around the infected plantations[2] although planned surveys are necessary to confirm this.[1]

In the U.S. and Canada, this species has proved to be moderately to highly resistant to the rust (Bingham, these proceedings).

PINUS PARVIFLORA

Indigenous at higher elevations throughout Japan.

This pine is moderately resistant to blister rust infection. The rust is recorded sporadically on exotic plantings in Great Britain and the United States (Spaulding, 1929). It is quite susceptible under artificial inoculation in the U.S. (Bingham, these proceedings).

INTRODUCED WHITE PINES IN ASIA

PINUS STROBUS L.

Plantations of this species were established 50 years ago in Korea and Japan. However, the plantations have remained free from blister rust disease in both countries. Dr. S. K. Hyun[1] states that in Korea, a rust believed to be *C. ribicola* was found on *Ribes fasciculatum* Sieb. et Zucc. about 50 meters from a *P. strobus* plantation that remained uninfected. *C. ribicola* is not recorded on *P. strobus* in Japan although the rust apparently occurs on *Ribes latifolium* Jancz., *R. rubrum* L. and *R. sachalinense* Nakai in that country.[3]

PINUS AYACAHUITE EHRENB.

This species has been tried both in the nursery and in the field in the Western Himalayas in India. No attack by *C. ribicola* is recorded, though the trees have not been thoroughly and repeatedly examined.

DISCUSSION

It is difficult to understand the absence of any authentic record of *C. ribicola* in Japan on indigenous or exotic 5-needle white pines, including the susceptible *P. strobus*. Apparently the rust is recorded on *Ribes* there. A similar situation occurs in Korea where 50-year-old plantations of *P. strobus* have remained free from blister rust infection nearby an infected *Ribes* bush. A different situation, however, exists in Korea where *P. koraiensis* (in plantations) is severely attacked by *C. ribicola*, and *Ribes* spp. possibly is absent around the infected pine. This may possibly be explained by autoecism (pine-to-pine spread) in the aecial stage of the rust, but autoecism has not been conclusively proved (Spaulding, 1922). More recent reports indicating autoecism (Scholz, 1960) seem to be disproved by failure of attempts to inoculate *P. strobus* by Boyer (1961). Our knowledge of the life history of the rust therefore appears incomplete. An intensive survey of the blister rust, and also

[2] *L. S. Yoon, personal communication, 1969.*
[3] *Dr. H. Saho, personal communication, 1969.*

inoculation experiments to determine the susceptibility of the various white pines and *Ribes* species appears necessary.

The aecial stage of *C. ribicola* on *P. wallichiana* was named *Peridermium indicum* Colley and Taylor (1927), because it was considered distinct from *Peridermium strobi* Klebahn, the aecial stage of *C. ribicola* on *P. strobus*. Bagchee (1950) found two distinct Peridermiums on *P. wallichiana* in India. One resembled *P. indicum* of Colley and Taylor with the alternate host being *R. rubrum*, occurring in Kulu and Chakrata. The other was similar to *P. strobi* with alternate host being *R. orientale* Poir. occurring further to the west in Kashmir. However, he considered this morphological difference inadequate for considering them distinct. Peterson (1967) maintains the separate identity of the two aecial stages occurring on *P. wallichiana* and *P. strobus* based on differences in aeciospore and peridial wall characters. In view of this, the occurrence of more than one strain in *C. ribicola* may have to be reexamined. Until now *C. ribicola* has been regarded as a homogenous species (Boyce, 1961) and is not known to occur in more than one strain on Ribes (Hahn, 1949). A critical morphological study of *C. ribicola* based on material collected from all over the world and cross inoculation experiments are necessary, as this may have a bearing on the relative blister rust resistance of 5-needle pines.

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FLOOR DISCUSSION

Discussion here concerns all 3 papers in the panel on "Relative Blister Rust Resistance of Native and Introduced White Pines of Europe and Asia," i.e., also for the preceding papers by Bent F. Søegaard and John Gremmen. Dr. Bakshi's paper was read by his coworker Dr. S. Kedharnath, since Dr. Bakshi was unable to attend the Advanced Study Institute.

HEIMBURGER: Mr. Gremmen points out that you must have healthy rootstocks if you would use grafts to test for resistance to white pine blister rust. This is a very important factor in our work in Ontario, and we handle it in the following way. We take potted, 4-year-old seedling stock and we graft them in the greenhouse as close to the ground as possible. Then we plant them out in a nursery the following spring, planting them deep so that the place of grafting is underground. Often new roots will come from the graft callus, and the original stock may die. Therefore, if the original rootstock had been infected with blister rust the danger of this disappears. This technique may be valuable in Mr. Gremmen's program for testing resistance of white pine.

BINGHAM: Dr. Søegaard, could you describe the nature of the blister rust bark lesions in your "class Z", where the branch was infected but the lesion died out?

SØEGAARD: The branches were successfully invaded by the rust, sometimes pycnia appeared, but aecia (in successive years) did not and eventually the cankers died.

BINGHAM: We've had some interesting suggestions in Dr. Bakshi's paper on the possible existence of autoecism in the white pine blister rust. I would like to address an inquiry to Dr. Hyun, concerning the *P. koraiensis* plantations where autoecism might be involved. Dr. Hyun, in the case mentioned where *P. koraiensis* became infected in the apparent absence of alternate host *Ribes* spp., how thorough a search of the plantation vicinity was made to ascertain that *Ribes* was absent?

HYUN: Yes, I think that is a very important question. The infected plantation was observed in 1967, 1968, and 1969. I'm not saying that absolutely no *Ribes* were present; possibly there were some. A thorough search was made of the plantation area and of the 500-meters surrounding it, yet we failed to find any.

VAN ARSDEL: I'd like to make a related comment here. One time, in the Mississippi River valley between Wisconsin and Minnesota (an area generally considered to be climatically free of blister rust), I found a white pine just covered with rust. I was very interested in the tree and observed it for several years. It was at the mouth of a canyon, or deep valley, where there was a nighttime cold air drainage. *Ribes* occurred high on the hill at a great distance. This kind of air drainage can occur, and it can carry quite a few *C. ribicola* spores in from a great distance. It can be very specific and hit one area.

BINGHAM: Yes, I would second this remark for distant infection of western white pine, based on studies by Merle Lloyd, formerly of my Experiment Station. We have similar, long-distance air drainage patterns, and apparently we can receive infection from great distances. However, like Dr. Hyun, I would hate to say we had no *Ribes* within these areas.

RELATIVE BLISTER RUST RESISTANCE OF NATIVE AND INTRODUCED WHITE PINES IN EASTERN NORTH AMERICA

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ABSTRACT

The main results at Maple, Ontario, Canada, with blister rust inoculation of seedling populations of *Pinus peuce*, *P. peuce* x *strobus*, *P. griffithii*, *P. griffithii* x *strobus*, *P. monticola*, *P. parviflora*, *P. strobus* x *pentaphylla* and *P. strobus* are presented.

Some *P. peuce*, *P. griffithii* and *P. parviflora* populations show high proportions of resistant seedlings and are of promise for further resistance breeding. Two *P. strobus*, differing in susceptibility, were used to identify good resistance transmitters in *P. peuce*. Several *P. griffithii* x *P. strobus* natural hybrid populations contain high proportions of resistant seedlings and indicate that their female parents may be good resistance transmitters. One *P. pentaphylla* was used to indicate somewhat higher resistance in Wisconsin and Canadian *P. strobus* selections than in unselected *P. strobus*. Breeding for resistance at the intraspecies level in *P. strobus* has thus far not been as promising.

The resistance of white pines to blister rust, caused by *Cronartium ribicola* J.C. Fisch. ex Rabenh., discussed in the following is resistance just to the races of blister rust introduced to both eastern and western North America from Europe and probably does not represent resistance to all possible races. It is probable that the blister rust in North America has undergone only slight changes in virulence since its introduction at about the turn of the century. It encountered very susceptible hosts, both in the pines and in some of the *Ribes*. Hence, the information about resistance of the white pines obtained in western Europe and in eastern and western North America should be quite comparable. Differences in infection frequency and intensity would be due more to differences in susceptibility of the hosts and conditions for infection than to possible differences in rust virulence.

Observations on resistance of the different white pines are thus far based only on very small samples of the total range of their variation. This applies particularly to observations on resistance of exotic species. Spaulding (1925), Hirt (1940), Childs and Bedwell (1948) and Patton (1966) have found the resistance of several Asiatic species to be higher than the resistance of the native *Pinus strobus* L. and *P. monticola* Dougl.

Earlier work with resistance breeding of white pine, particularly in Wisconsin, has been amply reviewed by Patton (1966) and will not again be reviewed here. Because of limitations of time and space, only the most important data on rust resistance of *P. strobus* and some of the related species and hybrids will be discussed in the following.

The white pine breeding project initiated in 1946 at the Southern Research Station of the Ontario Department of Lands and Forests at Maple, Ontario, Canada, includes the breeding of white pine for resistance to blister rust. The breeding for resistance to this rust was greatly stimulated by the findings of Riker and Kouba (1940), and Hirt (1948). In Canada, forest pathologists discovered a heavy attack of blister rust in a white pine plantation at the Seigniory of Mr. Joly de Lotbiniere at Pointe Platon, on the south shore of the St. Lawrence River, about 30 miles west of Quebec City. This plantation was established in 1908 with about 400 plants imported from a nursery in Germany. After heavy infection with blister rust and removal of all infected trees by 1945, there were 35 trees left that were completely free from any infection. These remained free from the disease during the following 10 years and have been used as a source of seeds and scions since then. Seedlings from this plantation have also been used to compare the resistance to blister rust of white pines of different origins (Heimburger, 1956). These studies indicated that the seedlots from Pointe Platon contained a greater proportion of healthy plants after heavy natural infection in a nursery than comparable seedlots from unselected trees.

The following method of inoculation with blister rust has been used: A seed bed is surrounded by a frame of lumber, the soil is moistened and ribes leaves with telial columns are stuck into the soil rather densely among the seedlings, with their petioles about 1/2 inch (1.2 cm) in the soil. The ribes are then watered down. Sections of ribes shoots with suitable leaves are used in the same manner as the above to inoculate older seedlings and grafts. The bed is covered with a lath screen and double thickness of wet burlap which is held down by another lath screen. The whole is kept moist for about a week with plastic hose sprinklers.

Black currant (*Ribes nigrum* L.) leaves are used as a source of inoculum. The currants are often infected so heavily by the rust that many leaves drop off during the hot weather of July-August and very few are available at the time of inoculation in September-October. This was remedied about 15 years ago by raising a few thousand seedlings of commercial varieties from berries bought on the market and by selection among these for rust susceptibility and good leaf retention during the summer drought period. About a dozen selected seedlings are being propagated by cuttings as a clone mixture. The currant bushes are cut down to the ground in the fall at the time of shoot and leaf collection for inoculation. This produces strong shoots with good leaves in the following year.

After 2 to 3 years in the inoculation bed, the healthy seedlings are set out in a nursery compartment at a rather wide spacing. After another 4 to 5 years in the nursery, the remaining healthy plants are set out in test areas. The climate at Maple is not favorable for inoculation with blister rust. Occasionally a short period of moist and cool weather, suitable for inoculation is available at about the end of August. After this there is usually a fairly long period of "Indian Summer" with warm, dry days, later followed by frosty nights when conditions are again favorable for inoculation in September-October.

Repeatedly, materials that remained healthy in the inoculation beds have shown blister rust infection in the nursery and in the test areas. This is especially the case with *P. strobus* and its hybrids with other species.

P. peuce Griseb. presents one of the simplest cases of rust resistance. The results of our tests are presented in Table 1. There are four populations, raised from seeds obtained from Finland, Yugoslavia, Bulgaria and Hungary. All populations contain some susceptible seedlings 2 to 6 years after inoculation. The population from Finland shows the largest proportion of resistant seedlings, 87%, and remains stable thereafter. The other populations show much lower proportions of resistant seedlings (19%, 33% and 47%). It is perhaps significant that the population from Finland, raised from seeds obtained from the arboretum Mustila, where blister rust is known to be present, shows the highest proportion of resistant seedlings and remains stable. Is this the result of natural selection for resistance after one generation of continued attack?

P. peuce x *P. strobus*.--The results of crossing 27 *P. peuce* clones with one "wild" *P. strobus*, the grafts of which were found susceptible to blister rust, are shown in Table 2. Only eight seedlings out of 278 were blister rust free 2 to 5 years after inoculation. Moreover, 6 of the 8 healthy seedlings later died of unknown causes--possibly due to blister rust.

The results of crossing 12 *P. peuce* clones with another "wild" *P. strobus*, the grafts of which remained resistant in our tests, are presented in Table 3. Seven of the resulting hybrid progenies remain stable after 2 to 3 years of inoculation, while 5 continued to segregate susceptible seedlings up to 8 years thereafter. The resistance varies from 3 to 42%.

P. griffithii McClell. (syn. *P. wallichiana* A.B. Jacks.)--Tests with seedlings of this species (Table 4) are confounded by the poor climatic adaptation of most strains to our growing conditions and the resulting great losses among the seedlings due to causes other than blister rust. Out of 125 seedlings of a provenance from E. Punjab (WP 78), one resistant seedling was obtained from among 3 survivors after 6 years of testing. Another population, from an elevation of over 11,000 feet in W. Pakistan, resulted in 31 resistant grafts among 32 survivors out of 105 original grafts. The scions for this population were collected, one from each plant, from young natural regeneration and subsequently grafted at Maple. In the 5 populations tested, resistance to blister rust varied from 23% to 97%, four populations remaining stable 3 to 7 years after inoculation, while one population continues to segregate susceptible seedlings. Unfortunately, the population with the highest resistance is a high-elevation type of poor growth form and growth rate. Several grafted clones obtained from parks, arboreta and botanical gardens are reasonably well adapted and flower profusely. It is possible that progeny tests with these, now in progress, will identify some good resistance transmitters for future breeding work.

P. griffithii x *P. strobus*.--The results of tests with these hybrids are shown in Table 5. All seedling populations sufficiently tested thus far are results of natural hybridization of *P. griffithii* with *P. strobus*. Of the 8 populations tested, 4 have been eliminated entirely, mostly by blister rust. The remaining 4 populations show resistance ranging from 15% to 46%, i.e., in some cases higher than in *P. griffithii*. It is possible that their female parents have been subjected to some natural

Table 1. Survival of blister rust inoculated seedlings from four populations of *Pinus peuce*

Populations	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings: Dead cause unknown	Fate of seedlings: Blister rust killed	Fate of seedlings: Clean (resistant)	Year of last obs. blister rust infection	% resistance	Seedlings alive in 1968[a]
Pinus peuce (WP 117-Finland)	10	1	1951,53,54,56	2	1	7	1957	87	6
P. peuce (WP 351-Yugoslavia)	33	2	1960,62,63,64, 65,66	16	9	8	1966	47	8
P. peuce (WP 352-Bulgaria)	73	3	1961,62,63,64, 65,66	36	30	7	1968	19	7
P. peuce (WP 925-Hungary)	6	2	1964,65,66,67, 68	2	4	2	1968	33	2
Total	122			56	44	24		35	23

[a] Decrease in seedling number due to death of seedlings by unknown causes.

Table 2.--Survival of blister rust inoculated *Pinus peuce* x *Pinus strobus* hybrid seedlings involving 27 *Pinus peuce* seed parents and pollen of one susceptible *P. strobus* tree (No. 5-784)

Populations	Total No. seedlings tested	Age of seedlings when first incoulated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resis-tance	Seed-lings alive in 1968[a]
				Dead cause unknown	Blister rust killed	Clean (resis-tant)			
WP 509	106	3	1962,64	17	88	1	1966	1	0
WP 510	2	4	1963	0	2	0	1966	0	0
WP 511	38	3	1962,63,64	5	33	0	1966	0	0
WP 512	5	4	1963	3	1	1	1966	50	0
WP 513	23	4	1963	1	20	2	1966	9	0
WP 514	1	4	1963	0	1	0	1966	0	0
WP 774	2	3	1963,64	0	2	0	1965	0	0
WP 775	17	3	1963,64	12	3	2	1965	40	0
WP 776	51	3	1963,64	33	18	0	1965	0	0
WP 777	2	3	1963,64	0	2	0	1965	0	0
WP 778	53	3	1963,64	33	20	0	1965	0	0
WP 779	2	3	1963,64	1	1	0	1965	0	0
WP 780	30	3	1963,64	26	4	0	1965	0	0
WP 781	1	3	1963	0	1	0	1965	0	0
WP 782	32	3	1963	20	12	0	1965	0	0
WP 783	55	3	1963	24	31	0	1965	0	0
WP 784	6	3	1963,64	1	5	0	1965	0	0
WP 785	1	3	1963,64	0	1	0	1965	0	0
WP 786	1	3	1963,64	0	1	0	1965	0	0
WP 787	12	3	1963,64	10	2	0	1966	0	0
WP 788	8	3	1963,64	4	4	0	1966	0	0
WP 789	17	3	1963,64	13	3	1	1966	25	1
WP 790	2	3	1963,64	1	1	0	1968	0	0
WP 791	14	3	1963,64	10	4	0	1966	0	0
WP 792	2	3	1963,64	0	2	0	1965	0	0
WP 794	11	3	1963,64	7	3	1	1965	25	1
WP 795	33	3	1963,64	28	5	0	1966	0	0
Total	527			249	270	8		3	2

[a] Decrease in seedling number due to death of seedlings by unknown causes.

Table 3. Survival of blister rust inoculated *Pinus peuce* x *Pinus strobus* hybrid seedlings involving 12 *Pinus peuce* seed parents and pollen of one resistant *Pinus strobus* tree (No. 5-13)

Populations	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resis-tance	Seed-lings alive in 1968[a]
				Dead cause unknown	Blister rust killed	Clean (resis-tant)			
WP 353	491	3	1960,61	46	433	12	1963	3	11
WP 354	83	3	1960,61	12	60	11	1968	16	11
WP 355	57	3	1960,61	0	42	15	1961	26	10
WP 356	169	3	1960,61	28	128	13	1962	9	8
WP 357	56	3	1960,61	5	44	7	1968	14	7
WP 358	102	3	1960,61	12	81	9	1965	10	7
WP 360	152	3	1960,61	8	136	8	1965	6	8
WP 361	35	3	1960,61	3	25	7	1968	22	7
WP 365	45	3	1960	10	21	14	1961	40	12
WP 366	44	3	1960,61	0	33	11	1962	25	9
WP 369	74	3	1960,61	2	63	9	1962	13	6
WP 372	34	3	1960,61	1	19	14	1962	42	12
Total	1342			127	1085	130		11	108

[a] Decrease in seedling number due to death of seedlings by unknown causes.

Table 4. Survival of blister rust inoculated seedlings from five populations of *Pinus griffithii*

Populations	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resistance	Seedlings alive in 1968[a]
				Dead cause unknown	Blister rust killed	Clean (resistant)			
WP 78	125	3	1951	122	2	1	1957	33	1
WP 123-133[b] (grafts)	105	2	1953	73	1	31	1957	97	28
WP 875	87	2	1963,64,65,66	41	11	35	1965	76	15
WP 876	114	2	1963,64,65,66	94	15	5	1966	25	5
WP 878	54	1	1963,64,65,66	32	17	5	1965	23	5
Total	485			362	46	77		63	54

[a] Decrease in seedling number due to death of seedlings by unknown causes.

[b] Grafted January 3, 1952, from scions collected from wild seedlings growing in Pakistan.

Table 5. Survival of blister rust inoculated hybrid seedlings of *Pinus griffithii* (8 trees) x *Pinus strobus* (wind)

Population	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resis-tance	Seed-lings alive in 1968[a]
				Dead cause unknown	Blister rust killed	Clean (resis-tant)			
WP 97 & 156	62	2	1953,54,56	49	11	2	1961	15	2
WP 138	486	2	1953,54,62	473	11	2	1965	15	2
WP 637 & 717	248	1	1961	139	38	71	1963	0	0
WP 139	176	2	1953,54	68	58	50	1965	46	50
WP 506	3	4	1963	0	3	0	1966	0	0
WP 140	63	2	1953,54	50	12	1	1960	8	0
WP 141	562	2	1953,54	474	75	13	1968	15	13
WP 507 & 640	7	2	1961,62,63	2	5	0	1966	0	0
Total	1607			1255	213	139		40	67

[a] Decrease in seedling number due to death of seedlings by unknown causes.

screening for climatic adaptation and resistance to blister rust, in a similar manner to what seems to be the case with some *P. peuce* in Finland. The most promising population thus far is W.P. 139, reasonably stable 3 years after inoculation and showing good adaptation and vigorous growth. Some trees of this population have begun flowering and are being used for breeding purposes.

P. monticola Dougl.--The results of tests with seedlings of this species, raised from seeds obtained in the Interior of British Columbia, are presented in Table 6. All 5 populations tested were eliminated by blister rust infection 6 to 8 years after inoculation. Poor adaptation to climate was also quite evident. In addition, there are 3 populations, not shown in the table. These have been subjected to natural infection by blister rust only. Two are still represented by 9 and 2 surviving seedlings, respectively. These seedlings have been grafted for further resistance tests. Because of the remarkable resistance of *P. monticola* materials to attacks by the white pine weevil, *Pissodes strobi* Peck, additional new materials have been obtained from British Columbia of the most promising provenances, as shown by former tests. The resulting seedlings will be screened for resistance to blister rust on a fairly large scale, prior to testing for weevil resistance. About 15 years ago seeds of some of R. T. Bingham's resistant selections were received at Maple. The 7 resulting seedling lots have all perished in about 6 years because of poor climatic adaptation.

P. parviflora Sieb. & Zucc.--The results with one population raised from seeds received from Nagano Prefecture, Honshu, Japan, are shown in Table 6. Five consecutive inoculations with blister rust have caused no infection. The losses are due entirely to other causes, mainly poor climatic adaptation. Seedlings of this species show very slow growth initially and many perish from frost heaving. It has not been possible to keep this population growing on its own roots. Since 1960 all the more vigorous seedlings have been grafted on *P. strobus*, resulting in a very satisfactory growth rate and few losses thereafter. No blister rust has been observed on these materials nor on any other grafts of *P. parviflora* and *P. pentaphylla* Mayr subjected to natural infection. It must be concluded that at least this population is highly resistant, if not immune, to blister rust. The same is the case with *P. koraiensis* Sieb. & Zucc., where only occasional needle spots of no further consequence have been observed after natural infection.

P. strobus x *P. pentaphylla*.--The blister rust infection of 5 seedling populations from this and the reciprocal cross with a single *P. pentaphylla* from Rochester, New York, is shown in Table 7. All populations show infection and one was eliminated 3 years after inoculation. Three of the remaining populations became infected 1 year after inoculation, while the fourth required 4 years for this. In all cases the populations continued to segregate susceptible seedlings for 1 to 5 years, i.e., they were unstable in this respect as are most hybrids with *P. strobus*. The results indicate that the susceptibility of *P. strobus* is incompletely dominant to the supposed resistance of *P. pentaphylla*. The resistant selections of *P. strobus* from Wisconsin and Pointe Platon in some cases yield progenies with somewhat higher proportions of rust-free seedlings than unselected *P. strobus* and have as yet not been eliminated by blister rust.

Table 6. Survival of blister rust inoculated seedlings of five populations of *Pinus monticola* and one population of *Pinus parviflora*

Population	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resistance	Seedlings alive in 1959
				Dead cause unknown	Blister rust killed	Clean (resistant)			
P. monticola WP 71	255	3	1951,53,54, 56,57	231	24	0	1959	0	0
P. monticola WP 72	64	3	1951,53,54,56	59	5	0	1957	0	0
P. monticola WP 74	249	3	1951,53,54,56	223	26	0	1957	0	0
P. monticola WP 75	14	3	1951,53,54	13	1	0	1957	0	0
P. monticola WP 76	55	3	1951	44	11	0	1958	0	0
Total	637			570	67	0		0	0
P. parviflora WP 120	1127	2	1953,54,55, 56,57	733	0	394		100	394

Table 7. Survival of blister rust inoculated hybrid seedlings of four crosses of *Pinus strobus* resistant, selected as resistant and unselected x *Pinus pentaphylla* plus one cross of *Pinus pentaphylla* x *Pinus strobus* (wind)

Cross	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings: Dead cause unknown	Fate of seedlings: Blister rust killed	Fate of seedlings: Clean (resistant)	Year of last obs. blister rust infection	% resistance	Seedlings alive in 1968[a]
P. strobus (res.) x *P. pentaphylla*	144	3	1962,63,64,65	83	60	1	1966	2	1
P. strobus (sel.) x *P. pentaphylla*	59	3	1962,63,64	10	46	3	1968	6	3
P. strobus (sel.) x *P. pentaphylla*	669	3	1962,63	356	309	4	1967	1	3
P. strobus (unsel.) x *P. pentaphylla*	159	3	1962,63	62	92	5	1966	5	4
P. pentaphylla x *P. strobus* (wind)	25	4	1963	19	6	0	1966	0	0
Total	1056			530	513	13		2	11

[a] Decrease in seedling number due to death of seedlings by unknown causes.

Table 8. Survival of blister rust inoculated F_2 seedlings of nine *Pinus strobus* crosses selected for resistance to blister rust

Population	Total No. seedlings tested	Age of seedlings when first inoculated	Inoculation years	Fate of seedlings			Year of last obs. blister rust infection	% resistance	Seedlings alive in 1967
				Dead cause unknown	Blister rust killed	Clean (resistant)			
WP 729	1	3	1963,64,65	0	1	0	1966	0	0
WP 730	100	3	1963,64,65,66	66	34	0	1967	0	0
WP 731	8	3	1963,64	4	4	0	1965	0	0
WP 732	100	3	1963,64,65	67	33	0	1967	0	0
WP 733	100	3	1963,64,65	44	56	0	1967	0	0
WP 735	19	3	1963,64,65,66	7	12	0	1967	0	0
WP 736	946	3	1963,64,65	549	397	0	1968	0	0
WP 737	244	3	1963,64	84	160	0	1967	0	0
WP 739	23	3	1963,64,65	7	14	2	1966	13	2
Total	1541			828	711	2		0.3	2

P. strobus.--The results of one series of progeny tests with selected clones from Pointe Platon are shown in Table 8. The crosses were made to obtain an F_2 generation of resistant seedlings for further breeding work and to evaluate 9 clones selected for resistance under conditions of heavy infection in the field and confirmed in our tests with grafts. As can be seen, the experiment was only partially successful. Only one clone showed promise of producing an F_2 generation while the other 8 clones yielded seedlings that were eliminated by blister rust 3 to 6 years after inoculation. Most of these were populations with unstable resistance, i.e., they continued to segregate susceptible seedlings up to 4 years before being eliminated by blister rust. Most of our other crosses within *P. strobus* are as unsatisfactory from a resistance breeding standpoint as those mentioned above. Selected materials usually have some resistance for a year or two after inoculation, but then the populations are eliminated by rust or segregate susceptible seedlings in succeeding years, leaving only very few plants for further work.

This indicates, perhaps, that the inoculation method has not been adequate to evaluate resistance and a more intensive method for infection is needed. It is probably also an expression of an interaction of resistance and environment. Another possible reason for the segregating seedling populations so often observed in screening *P. strobus* for resistance is simply the lack of certain resistance genes in this species. If this is the case, the introduction of such genes from other species may be the only way to form a reasonably realistic breeding program with *P. strobus*.

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FLOOR DISCUSSION

Panel leader Bingham withheld discussion of this paper until after the closely related paper by Bingham, immediately following.

TAXONOMY, CROSSABILITY, AND RELATIVE BLISTER RUST RESISTANCE OF 5-NEEDLED WHITE PINES

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ABSTRACT

White pine speciation is summarized, and information on interspecies crossability is assembled. The literature on the extent of white pine blister rust (*Cronartium ribicola*) infection in species trials of 5-needled Subsections *Cembrae, Balfourianae,* and *Strobi* white pines is reexamined, and combined with observational data on infection of these pines in Europe. This existing evidence, plus new evidence compiled at the author's station in northern Idaho, is arrayed and analyzed to provide a tentative ranking of blister rust resistance among 14 of the more than 20 5-needled white pines. The ranking, along with the consolidated and updated information on botanical ranges and crossability of white pines should be useful in the planning of future white pine blister rust resistance breeding.

INTRODUCTION

Establishment of a Committee on White Pine Blister rust has revived international interest in blister rust resistance of the world's white pines. This is one of six Committees established by Henry D. Gerhold, Chairman of the IUFRO Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects.

There are more than 20 of these 5-needled white pine species--several of them are quite inaccessible and not very well known. These species constitute a broad range of breeding materials for use by the resistance breeder against white pine blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.). At present the resistance breeder cannot even secure, much less work with, all of these species. However, he can direct his program toward those species exhibiting the widest adaptation and the strongest, species-wide resistance. He may be particularly interested in white pines that have evolved near the presumed Eurasian gene center(s) of the rust organism; these pines coexist with the rust in more or less balanced host-parasite systems, indicating possible existence of long-lasting "horizontal" or "uniform" resistance in these species (see van der Plank, 1969; Hoff and McDonald, these proceedings).

A critical examination of the relative blister rust resistance of these white pines is needed as a research tool for the introduction and testing of new white pine species. Also, where the breeder is seeking to improve resistance of susceptible but otherwise locally adapted and important native white pines, an updating of information on interspecies

crossability amongst 5-needled white pines will be needed. The objective of this paper is to meet these two needs.

The 5-needled white pine species discussed herein are identified according to the usage of Critchfield and Little (1966); this taxonomic treatment for white pines has been accepted by the IUFRO Committee on (resistance to) White Pine Blister Rust, for use in all future communications.

WHITE PINE TAXONOMY, BOTANICAL RANGE, AND CROSSABILITY

Shown in Table 1 are the 21 5-needled white pines of *Pinus* Subsections *Cembrae*, *Strobi*, and *Balfourianae*; the Latin names and authority are as given by Critchfield and Little (1966). Also shown in the table are: synonomy; common names; botanical ranges; and interspecies crossability.

The only additional information required here concerns two taxonomical problems that are confounding clear communications between white pine breeders. These problems are: (1) the controversy over which Latin binomial (*P. griffithii* McClelland or *P. wallichiana* A. B. Jackson) is correct or preferred for the Himalayan "blue pine"; and (2) the question as to whether the "Japanese white pine" complex (*P. parviflora* Siebold and Zuccarini) should be separated into a northern taxon (*P. pentaphylla* Mayr) and a southern taxon (*P. pentaphylla* var.*himekomatsu* Makino or *P. himekomatsu* Miyabe & Kudo). The two taxa fall in distinct populations separated by an easily located zone of contact and introgression, as recognized by many Japanese botanists and dendrologists. Resolution of these two problems was requested of the International Association for Plant Taxonomy, August 18, 1969, by the Committee on White Pine Blister Rust.

RELATIVE BLISTER RUST RESISTANCE OF 5-NEEDLED WHITE PINES

A composite, tentative ranking of blister rust resistance for 14 white pines of Subsections *Cembrae*, *Strobi*, and *Balfourianae* is presented at the far right of Table 2. The ranking is based upon the observations and experiments of five independent observers; data in Table 2 are referenced to the observer's publications. However, to help the reader to perceive the relative weight of the data, and understand how observations were converted into the numerical ratings of the table, the extent of each observer's data and its conversion to numerical rankings is outlined below.

Spaulding, 1925 and 1929: Spaulding's observations cover his own earlier observations (Spaulding, 1922, and Pennington, *et al.*, 1921), plus those of von Tubeuf (1897 and 1917), Moir (1924), Clinton (1919) and Clinton and McCormick (1919). They are based on rust canker occurrence on a large number of white pines growing in natural stands or planted in a large number of localities in Europe and North America as follows: 4 *P. albicaulis* trees in 3 localities; 7 *P. aristata* in 5 localities; 31 *P. armandii* in 5 localities; 14 *P. ayacahuite* in 7 localities; 11 *P. balfouriana* in 8 localities; 1,000+ *P. cembra* and/or *P. sibirica* in 33 localities; 340+ *P. griffithii* in 38 localities; 950+ *P. flexilis* in 19 localities; 8 *P. koraiensis* in 8 localities; 28+ *P. lambertiana* in 9 localities; 120+ *P. monticola* in 15 localities; 34+ *P. parviflora* in 10

localities; 220 + *P. peuce* in 10 localities; and many thousands of *P. strobus* trees in more than 100 localities. Spaulding's (1925, Table 1) ratings of "Immune, Resistant, Susceptible, and Very Susceptible" are here merely ranked 1, 2, 3, and 4, respectively. Questionable rankings are given where Spaulding (1925) indicates the tree basis is weak.

Hirt, 1940: Hirt's observations were made on two field plots at Warrensburg and Syracuse, New York. Seedlings of the white pine species were planted in a systematic mix and exposed to natural inoculation by rust spreading from planted *Ribes nigrum* L. bushes. After a single season's exposure seedlings were lifted and held elsewhere for development of rust symptoms. Groups of from 44 to 100 seedlings each of 3-7 species were exposed in experiments undertaken in four different years. Intensity of infection was stated in terms of percentage of trees infected, numbers of cankers per infected tree, or cankers per 1,000 inches of needlage. Seedlings actually tested included: 68 *P. aristata* seedlings exposed for 2 seasons; 83 *P. cembra* for 1 season; 258 *P. flexilis* for 3 seasons; 72 *P. koraiensis* for 1 season; 174 *P. monticola* for 4 seasons; 322 *P. peuce* for 4 seasons; 56 *P. strobiformis* for 1 season; and 351 *P. strobus* for 4 seasons. Rankings given in Table 2 were obtained by assigning the lowest infection level (of all 3 measures of infection) the rank 1; the highest infection level, the rank 8; then, by arithmetically averaging the rankings.

Bedwell and Childs, 1943; and Childs and Bedwell, 1948: Bedwell and Childs reported upon levels of natural infection (cankers per thousand needles) in 159 pairs of *P. albicaulis* and *P. monticola* trees (heights ranged from 5 to 11 feet) growing together in 8 Idaho, Washington, and Oregon natural stands; also, these authors reported upon natural infection of 355 *P. albicaulis* and 1,077 *P. monticola* seedlings that were growing together in a Garabaldi, British Columbia, nursery. Later, Childs and Bedwell (1948) reported upon natural infection found on 7 experimental plots established in British Columbia and Oregon, mostly with 4-year-old nursery stock. Infection intensity, stated in terms of number of cankers per million seedling needles, was determined 5 to 10 years after outplanting on: 255 *P. aristata* trees located on 3 different plots; 42 *P. armandii* on 2 plots; 538 *P. flexilis* on 5 plots; 229 *P. griffithii* on 2 plots; 109 *P. koraiensis* on 1 plot; 447 *P. lambertiana* on 4 plots; 1,946 *P. monticola* on 7 plots; 369 *P. peuce* on 3 plots; 241 *P. strobiformis* on 3 plots; and 725 *P. strobus* on 5 plots. In addition, Childs and Bedwell observed natural infection on 4- to 40-feet-tall white pines in a Carson, Washington, arboretum, there examining 20 *P. aristata*, 2 *P. armandii*, 24 *P. flexilis*, 19 *P. griffithii*, 20 *P. koraiensis*, 11 *P. lambertiana*, 21 *P. monticola*, 22 *P. parviflora*, 3 *P. peuce*, 30 *P. strobiformis*, and 8 *P. strobus* trees. Rankings of Table 2, column 4, for the nursery and field plots or stands, come from converting the lowest level of cankers per million needles to rank 1, the highest to the highest numerical rank. For the Carson arboretum trees, rankings are in the order of susceptibility given by Childs and Bedwell.

Meyer, 1954: Meyer's observations are the most limited, coming from natural infection of single trees of 7 white pine species growing in a Hann. Münden, Germany, arboretum. The 20+-year-old trees were classified merely as without infection, or as weakly, moderately, or heavily infected. In Table 2 rank 1 applies to noninfected trees; ranks 2, 3, and 4 apply to the weakly, moderately, and heavily infected trees, respectively.

Table 1.--Taxonomy,[1] synonomy, botanical range, and crossability of 5-needled white pines in Subsections Cembrae, Strobi, and Balfourianae

SECTION SUBSECTION Species	Authority	Abbr.	Synonomy and common names	Native botanical range[2] (COUNTRY, with States, Provinces, or other political subdivisions)	Known interspecies crossability[3] (V=Verified hybrids, U=Uncertain or putative hybrids with seed or seedlings produced repeatedly, F=repeated failure)
STROBUS					
CEMBRAE					
Pinus albicaulis	Engelmann	P.al.	"Whitebark pine"	CANADA--Cent. & So. B.C. & S.W. Alta. USA--W.Wash., W. & N.E. Ore., N. Calif., W.Cent., N.W., & N.E. Nev., N. & Cent. Ida., W. Mont., N.W. Wyo.	U--P.fl.,mt., F--P.arm.,ay.,ko., la.,pa.,stb.,st.
Pinus cembra[4]	Linnaeus	P.ce.	P.cembra var. helvitica Hort, "Swiss stone pine," "Zirbe," "Arve"	S.E. FRANCE, S. SWITZERLAND, N. ITALY, extr. S. GERMANY, AUSTRIA, extr. N.W. YUGOSLAVIA, S.E. CZECHSLOVAKIA, Cent. & N. ROUMANIA, & USSR, UKRAINE, along Alps and Carpathian Mtns.	U--P.al.,mt., F--P.arm.,ay.,fl., gr.,ko.,la.,mt.,pa.,pe.,st.
Pinus koraiensis*	Siebold & Zuccarini	P.ko.	"Korean pine"	KOREA, N.E. CHINA--Antung, Kirin, S.E. Lisopeh, Sungiang, Hokiang, S.E. Heilungkiang, USSR--W. of Ussuri Riv. into Sikhote Alin Mtns. & N. of Amur Riv. into Buriensky Mtns., JAPAN--Cent. Honshu, N. Shikoku.	V--P.la., U--P.arm.,mt.,st., F--P.al.,ce.,fl.,gr.,pe.
Pinus pumila*	Regel	P.pu.	P.cembra var. pumila Regel, "Japanese stone pine"	Extr. N.W. MONGOLIA, USSR--E. Cent. & E. Siberia, Kamchatka Pen. & Sakhalin & Kurile Islands, N.E. CHINA, N. & Cent. KOREA, and JAPAN--Hokkaido & N. & Cent. Honshu.	U--P.al., F--P.fl.
Pinus sibirica*	Du Tour	P.si.	P. cembra var. sibirica Mayr, "Siberian stone pine"	USSR--N. Kola Pen., Ural Mtns. through W. to Cent..E. Siberia, N. MONGOLIA, and extr. N. Sinkiang Prov. of CHINA	U--P.al., F--P.arm.,fl.,gr.
STROBI					
Pinus armandii*	Franchet	P.arm.	"Armand pine" (includes var. amamiana Koidz.	W. & S.W. CHINA--Shensi, Kansu, Honan, Szechwan, Kwangsi, Yunnan, Kweichow Provs. & Hainan Island, N. BURMA, extr. N.E. INDIA, S.W. TIBET, TAIWAN, & S. JAPAN islands (v. amamiana Yaku & Tanega Shima	V--P.la., U--P.ko., F--P.al., ce.,fl.,gr.,mt.,si.,stb.,st.
Pinus ayacahuite	Ehrenberg	P.ay.	Includes vars. ayacahuite Ehrenb. & veitchii Shaw, "Mexican white pine"	S. MEXICO and eastward into S.W. GUATEMALA, W. HONDURAS, & N.W. EL SALVADOR	V--P.fl.,gr.,st., F--P.al.,ce., la.
Pinus dalatensis*	de Ferré	P.da.		S. VIETNAM	
Pinus fenzeliana*	Handel-Mazzetti	P.fe.	P.parviflora var. fenzeliana Wu, P. kwangtungensis Chun	CHINA--W. Kwangsi, S. Hunan, N. Kwangtung Provs. & S. Cent. Hainan Island, W.-Cent. VIET NAM	
Pinus flexilis	James	P.fl.	"Limber pine"	CANADA--S.W. Alta. & S.E. B.C., USA--extr. N.E. Ore., Cent. & S. Ida., W. Mont., N.W. & S.E. Wyo., Utah, Nev., Cent. E. & S. Calif., Cent. Colo., N. Cent. N.Mex., N. Cent. Ariz., & extr. S.W. N. Dak., S. Dak., & Nebr.	V--P.ay.,gr.,mt.,stb.,st., U--P.al., F--P.arm.,ce.,ko.,la., pa.,pe.,pu.,si.
Pinus griffithii*	McClelland	P.gr.	P.wallichiana A.B.Jack., P.excelsa Wallich, "Blue pine"	W. AFGHANISTAN and E. along Himalaya Mtns. through N. to extr. N.E. INDIA, N.W. PAKISTAN, NEPAL, extr. S. TIBET, BHUTAN, N. BURMA, and CHINA at Burma-N.E. India border.	V--P.ay.,fl.,mt.,pe.,pe.,st., F--P.arm.,ce.,ko.,la.,si.

Pinus lambertiana	Douglas	P.la.	"Sugar pine"	USA--S. Cent. Ore., N. Calif., and down Sierra Nevada Mtns. to S. Calif., MEXICO--N. Baja California State	V--P.arm.,ko., F--P.al.,ay.,ce., fl.,gr.,mt.,pa.,pe.,stb.,st.
Pinus morrisonicola	Hayata	P.mo.	P.formosana Hayata, P. formosensis Hayata, "Taiwan white pine"	TAIWAN, generally below P. armandii in elev.	
Pinus monticola	Douglas	P.mt.	"Western white pine"	CANADA--extr. S.W. Alta. & S. B.C., USA--W. Wash., N. Ida., W. Mont., N.E. & W. Ore., N. Calif. & extr. W.-Cent. Nev.	U--P.al., ce.,ko., V--P.gr.,fl., pa.,pe.,stb.,st., F--P.arm.,la.
Pinus parviflora	Siebold & Zuccarini	P.pa.	P.pentaphylla Mayr, P. pentaphylla var. himekomatsu Makino or P. himekomatsu Miyabe & Kudo, "Japanese white pine"	JAPAN--(var. pentaphylla) Cent. & N. Honshu & Sado Is., S. Hokkaido & Okushiri Jima Is.; (var. himekomatsu) Cent & S. Honshu, Shikoku, Kyoshu & Tsu Shima Is., KOREA--Ullung-do (Dagelet or Utsurio-To) Island.	V--P.gr.,mt.,pe.,st., F--P.al., ce.,fl.,la.
Pinus peuce*	Griesebach	P.pe.	P.excelsa Hooker, "Balkan pine"	W. Cent. & S.W. YUGOSLAVIA, E. Cent. & N.E. ALBANIA, W. Cent. & S.W. BULGARIA, & extr. N. GREECE.	V--P.gr.,mt.,pa.,st., F--P.ce., fl.,ko.,la.
Pinus strobiformis	Engelmann	P.stb.	P.flexilis v. reflexa Engelm., P.ayacahuite v. brachyptera Shaw, "Southwestern white pine"	USA--Extr. S. Cent. Colo., Cent. & W. N.Mex., Cent. & E. Ariz., & W. Tex., MEXICO--N. Mexico south to Zacatecas & San Luis Potosi States	V--P.fl.,mt., F--P.al.,arm.,la.
Pinus strobus	Linnaeus	P.st.	"Eastern white pine"	CANADA--Newfoundland, S. Quebec, S. Ontario, to extr. S.E. Manitoba, USA--New England States W. to Minn., Wisc., N.E. Iowa, N. Ill., W. Ind., and S.W. down Appalachian Mtns. to Ky., Tenn., and extr. N. Ga. & N.W. S.Carolina.	U--P.ko., F--P.al.,arm.,ce.,la., V--P.ay.,gr.,fl.,mt.,pa.,pe.
var. chiapensis	Martinez	P.ch.	P.chiapensis(Martinez) Andresen, "Chiapas pine"	S. MEXICO and W.-Cent. GUATEMALA	
Pinus wangii*	Hu & Cheng	P.wan.		CHINA--S.E. Yunnan Prov.	
PARRYA					
BALFOURIANAE					
Pinus aristata	Engelmann	P.ari.	"Bristlecone pine"	USA--E. Cent. Calif., Cent. & S.E. Nev., Utah, Cent. Colo., and N. Cent. Ariz. & N.Mex.	V--P.ba., F--P.mt.
Pinus balfouriana	Greville & Balfour	P.ba.	"Foxtail pine"	USA--N.W. and E. Cent. Calif.	F--P.mt.

1/ Taxonomy follows that of Critchfield and Little (1966).

2/ Botanical range from Critchfield and Little (1966), modified by Mirov (1967).

3/ Crossability data for Section Strobus comes from Bingham, Hoff, and Steinhoff (in press); and for Section Parrya from unpublished data of the Institute of Forest Genetics, Placerville, California, and of this station.

4/ Asterisk denotes species that may have evolved near the Eurasia gene-center(s) of C. ribicola.

Table 2. Blister rust resistance rankings for 5-needled white pines

Species	Rankings (in order of increasing susceptibility) by 5 independent observers: Spaulding 1925 & 29	Hirt 1940	Bedwell & Childs 1943: Childs & Bedwell 1948 Pacific NW	Bedwell & Childs 1943: Childs & Bedwell 1948 Carson, Wn.	Meyer 1954	Bingham & staff 1954-69 data	Tentative average ranking
Pinus armandii	?[a] 1		1	? 1		3	1
P. cembra	2	1			2	2	1
P. aristata	? 2	2	1	1			1
P. griffithii	2		2	1	1	5	2
P. koraiensis	? 2	3	1	1		1	2
P. peuce	1-1/2[b]	5	3	? 1	1	4	3
P. sibirica	3						? 4
P. parviflora	? 2			1		6	5
P. strobiformis	? 3	4	4	3			6
P. strobus	3	6	5	? 4	4	8	7
P. flexilis	4	7	6	2	4	9	8
P. monticola	4	8	7	6	3	7	9
P. lambertiana	? 3		8	7	4		10
P. albicaulis	? 4		9	? 5			11
P. balfouriana	? 2			Mod. susc.[c]			?
P. ayacahuite	? 3						?

Resistant → Susceptible

[a] "?" indicated that ranking is based on relatively few places of observation or on a small number of test trees.
[b] 1925 ranking as amended in 1929.
[c] Cankers "common on 6-year-old transplants...in nursery beds."

Bingham and staff, 1954-1969: These new data, presented in the next to last column of Table 2, are based upon artificial inoculations of 2-year-old seedlings of 9 species including: 2 provenances of *P. armandii* with 63 seedlings; 4 of *P. cembra* with 32 seedlings; 12 of *P. flexilis* with 370 seedlings; 5 of *P. griffithii* with 194 seedlings; 3 of *P. koraiensis* with 39 seedlings; 305 of *P. monticola* with 30,000+ seedlings; 2 of *P. parviflora* with 13 seedlings; 4 of *P. peuce* with 34 seedlings; and 6 of *P. strobus* with 285 seedlings. The strength of this data lies in the fact that most often three or more provenances of a given species were tested. Rankings are based on percentage of seedlings infected, with rank 1 being the least heavily infected, rank 9 the most heavily infected. In all species at least a few seedlings became infected.

The "tentative average rankings" for blister rust resistance (last column, Table 2) are arithmetic averages of the rankings shown for the six observations of the five observers. Questionable rankings received a weight of 1/2.

CONCLUSIONS

SPECIES DESERVING IMMEDIATE ATTENTION

The IUFRO Committee on (resistance to) White Pine Blister Rust selected *Pinus griffithii* as their first choice for immediate attention (see Committee report, these proceedings) because of the following: its good performance and relatively high level of resistance exhibited in central and southern Europe and the U.S.A.; its extensive range and, thus, probable great genetic variability for resistance, growth, and hardiness. The Committee has also recommended that, as soon as possible, similar attention should be directed toward the moderately resistant *P. peuce* (also possibly having early-flowering genes, cf. Heimburger, these proceedings) as well as toward the highly resistant but inaccessible southeast Asian species *P. armandii* and *P. koraiensis*. The author is in complete agreement with these recommendations, including the suggestion that there should be a revival of white pine species-blister rust resistance trails in rust hazard areas of North America, Europe, and Asia.

OTHER SPECIES DESERVING MORE ATTENTION

Four other white pines, three of them little-known southeast Asian species related to *P. parviflora* or *P. griffithii* (cf. Critchfield and Little, 1966), deserve more attention that they have received in the past. The first of these is *P. strobiformis* from high elevations in the southwestern U.S.A. and northern Mexico. Certain provenances of this species have good growth potential and have proved to be winter-hardy throughout the U.S.A. (see Steinhoff, these proceedings). Resistance appears to be well above expectation (Table 2), and needs to be confirmed by better and wider testing. Its potential for direct planting, or as a source of resistance, deserves attention in northern European and North American rust hazard areas. The other three almost unknown species deserving more attention are the inaccessible southeast Asian white pines: *P. dalatensii*, possibly a relative of *P. griffithii*; *P. fenzeliana*; and *P. wangii* of the *P. parviflora* complex. Although possibly cold-sensitive, slow-growing, and of unknown blister rust resistance, these three white pines could become highly valuable sources of resistance. *P. wangii* and *P. fenzeliana* grow nearest to any *P. armandii*-*P. griffithii* blister rust gene-center.

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FLOOR DISCUSSION

Moderator Bingham withheld floor discussion on the previous, closely related paper by Dr. Heimburger so both papers could be discussed together, here.

GERHOLD: Mr. Bingham, would you like to comment on the correlation between blister rust infection in nursery tests and infection that you find after field exposure?

BINGHAM: Our information on this point is only now beginning to come in. Because I know Dr. Ronald Dinus will be presenting much more conclusive data on this point, with fusiform rust, tomorrow, I would

prefer to have him answer the question then (see Dinus, these proceedings).

KINLOCH: Can you clarify the basis for the blister rust resistance rankings of white pine species shown in your Table 2? I'm wondering particularly about the relative rankings of sugar pine (*Pinus lambertiana*) and western white pine (*Pinus monticola*). Recently I have seen some data from U.S. Forest Service, Region 6, the Dorena Project, indicating that under artificial inoculation sugar pine develops relatively few needle lesions as compared to western white pine.

BINGHAM: Observations on the relative resistance of the two species here at Moscow are nil. (Notice that the table indicates no comparative observations on sugar pine by Bingham and staff.) And what good information there is in the table is not based upon needle lesions, but upon bark cankers per million needles, from Bedwell and Childs. I would suggest that Mr. Gerald Barnes of the Dorena Project answer your question.

BARNES: We completed our first blister rust needle lesion or needle-spot tally on sugar pine and western white pine control-pollinated, intra-species crosses at Dorena (Cottage Grove, Oregon) in the spring of 1969. Dr. Kinloch is right; one of the firmer results of the examination was that the sugar pines on the average had fewer needle spots than the western white pines. The data showed something like 0.4 needle lesions per lineal inch of western white pine needles as compared with 0.1 lesions for sugar pine.

VAN ARSDEL: Have you shown a relationship between the amount of needle spots or flecks and the amount of bark cankers that result, so that you know the relation of spots and cankers is a true one?

BARNES: No, we have not as yet.

BINGHAM: Mr. Barnes, I believe your remarks on relative needle spotting of the two pines were based on data from full- or half-sib progenies from phenotypically resistant trees in heavily rusted natural stands. Is that correct?

BARNES: Yes, but my remarks also extended to the sugar and western white pine control (presumably unselected, non-resistant) seedlings examined in the same tests. The controls gave a similar result--fewer spots on the sugar pine needles.

BINGHAM: Then, perhaps, Dr. Van Arsdel, the lesser spotting of the sugar pine needles may be a species-wide character. There may simply be a higher level of foliar resistance in sugar pine, but other resistance-genes coming into play later in the development of pine:rust association may be absent, or less effective.

MCDONALD: Returning to Dr. Van Arsdel's question on the correlation between needle spotting and canker formation, I have completed a preliminary analysis on this and results indicate one spot per seedling is enough to cause one canker. Thus the correlation of frequency of needle spots with presence or absence of bark cankers breaks down. One needle spot per seedling is as likely to produce a recognizable canker as 100 spots per seedling are. In other words frequency of needle spotting could vary greatly without variation in the probability of cankering on a whole seedling basis.

VAN ARSDEL: Could I rephrase the question?* Do you get cankers without needle spots, because we did get them with eastern white pine (*P. strobus*)? In fact, I have always considered the needle spots as sort of a resistance reaction. In other words, only some of the successful infections result in needle spots, and some that don't result in spots might be causing the bark cankers you are seeing.

MCDONALD: In our preliminary analysis I mentioned above, 99.6% of the seedlings had needle spots we judged to be associated with successful attack by *Cronartium ribicola*. Thus, we had little opportunity to observe cankering in the absence of spotting.

BINGHAM: Maybe I can shed a little light on the problem, Dr. Van Arsdel. In certain of our annual, artificial inoculation runs, those that have been less successful than the one Dr. McDonald discussed, there has been a very good correlation between the presence of needle spots and cankers or the absence of needle spots and the absence of cankers. Perhaps your own Phytopathology publication, demonstrating that succulent *Pinus strobus* stems could be infected in the absence of needles (cf. Van Arsdel, E. P. Phytopathology 58: 512-514, 1968) might provide a partial explanation to the phenomenon of cankers sans needle spots. Now I have a question for you. Have you observed similar, unexplained cankers in the in the non-needled portion of stem internodes in nature?

VAN ARSDEL: Yes.

BINGHAM: Then you suspect that with *Pinus strobus* the phenomenon is also happening in nature.

VAN ARSDEL: Yes.

GERHOLD: I'm not sure that Dr. Kinloch's question was fully answered. Were different resistance criteria used by various investigators, and how were these taken into account when you established resistance rankings for the white pine species?

BINGHAM: In the Table 2 mentioned previously, results from Hirt, or from Bingham and staff were expressed in percent of trees in the different species that became infected in a given period of years. Bedwell and Childs' data were based upon number of bark cankers per million needles, but Spaulding's and Meyer's data were largely observational. If the "tentative average blister rust resistance rankings" of the last column of the table have any reliability, it comes from similarity of rankings found by the 3 investigative teams who gave quantitative results.

VAN ARSDEL: I have made a similar ranking, based on about the same literature as Mr. Bingham's. I included Stuart Moir's bulletin (Moir, W. Stuart. 1924. White-pine blister rust in western Europe. USDA Bull. 1186, 32 p.), and, as you know, I have written to obtain your rankings. Except for 2 or 3 of these species with "muddy" coverage, our rankings by literature review methods are very similar. Perley Spaulding and others have published the same relationship for *P. albicaulis* and *P. lambertiana* in Europe, that you showed here.

EXCHANGING AND CONSERVING TREE BREEDING MATERIALS

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ABSTRACT

Breeding for rust resistance, as for any other characteristic, requires access to a variety of genetic materials. International cooperation is needed in the exchange and conservation of germ plasm of forest trees. Problems of the breeder in obtaining the plant material he requires are numerous. International organizations helpful in overcoming these obstacles include the Food and Agriculture Organization of the United Nations, the International Union of Forestry Research Organizations and others. Examples of National efforts that have contributed to meeting the needs of forest tree breeders are given. The lesser need for conservation of germ plasm in forestry than in agriculture is explained. Some tree species in danger of extinction or of genetic change are listed, and the need for conservation of others is discussed.

INTRODUCTION

To breed for rust resistance or any other characteristic of a high-yielding variety of trees, the breeder must have access to a great variety of genetic materials. These include not only the varieties and provenances of the species with which he is primarily concerned, but also the related species from which desirable traits might be introduced. Of equal importance are non-related species having desired traits, like rust resistance. These might be introduced as exotics where rusts or other pests limit the growth of native species. Acquiring these diverse genetic materials is essential to the success of most breeding programs.

In recent years, several meetings have stimulated interest and led to improvement in our institutions and procedures for exchanging and conserving germ plasm of forest trees. This paper relates to the international aspects of this activity.

International movement of materials for forest tree breeding has accelerated rapidly in recent years as tree breeding programs have expanded. Breeders recognize the importance of exchanging material. They make extensive use of many species, provenances and selections in their breeding to produce high-yielding varieties. Breeders are concerned not only with resistance to rust or other pests but also with other desirable traits. They seek rapid growth, good form and superior wood qualities to name a few.

Anyone who has tried to obtain materials from other regions, particularly from other nations or continents, knows the problems very well. In many cases, the species that one desired is not well known in its native land, or one may not know the persons who are most knowledgeable about the species. Potential seed collectors are often completely unknown outside their local areas. Very often skilled collectors of seed or pollen are not available. Those able and willing to make collections may not have the resources to fill one's needs. Funds may not be available. Barriers to international monetary exchange may preclude providing funds. Equipment for cone or fruit collection, seed or pollen extraction may not be available or may not even exist in the country.

Unfavorable national attitudes may also stand between the breeder and the materials he wants. In some cases, political curtains preclude all communications. A few countries have prohibited exporting any seed of certain species to protect future national interests in forest production. Hopefully, such obstacles will dissolve before too long.

International quarantines often pose a very large, but never an insurmountable obstacle. Breeders must recognize the risks and potential losses from international transfer of diseases or insect pests. Risks of introducing a foreign disease are particularly high when vegetative reproductive material like seedlings, cuttings, or even pollen must be transported. Whenever possible, germ plasm should be transmitted as seed with appropriate sanitary procedures. The International Association of Plant Quarantine Officials constantly strives to improve procedures for detecting and preventing the transmission of undesirable diseases and pests. However, they also recognize the great importance of introducing valuable forest tree germ plasm.

Most officials have shown a willingness to cooperate in arranging for needed movements of forest tree materials. As yet, I have not encountered an insurmountable quarantine problem. Preplanning is the key to avoiding problems. Anyone contemplating international movement of plant material should carefully investigate the quarantine requirements of both the exporting and the importing countries. All potential problems should be solved to the satisfaction of the officials and the tree breeder. Only then should collections and shipments start.

In this country, introductions of potentially diseased vegetative material can be expedited by growing the material under post-entry quarantine until officials are satisfied that no diseases or insects have been introduced. Where quarantine facilities are neither suitable nor available for the handling of a particular introduction, facilities with an adequate safeguard can be developed inexpensively. Introductions of beneficial mycorrhizal fungi can pose a serious problem because of hazards of introducing soil or tree roots infected with dangerous organisms. This problem can best be solved by growing and importing desirable fungi in pure culture.

INTERNATIONAL ORGANIZATIONS

As one might expect, international organizations often are in the best position to solve international problems. The United Nations, the International Union of Forestry Research Organizations (IUFRO), and other international and multinational organizations are providing leadership and assistance. With their help and sponsorship the exchange and conservation of forest tree breeding materials are moving ahead.

FAO

The Food and Agriculture Organization (FAO) of the United Nations has numerous activities and gives strong leadership in this area. This organization serves its member Nations, but all other members of the United Nations may participate in and benefit from its activities as observers. Recently FAO, in cooperation with the International Biological Program (IBP), held a Technical Conference on the Exploration, Utilization, and Conservation of Plant Genetic Resources.

This Conference was concerned over the fact that the genetic resources of the plants by which we live are dwindling rapidly and disastrously. Attention was called to the fact that,

> "reserves of genetic variation...in the primeval forest equipped with a seemingly inexhaustable range of variation, have been or are being displaced by high-producing and uniform cultivars, and by forest plantations...This 'erosion' of our biological resources may gravely affect future generations which will, rightly blame ours for lack of responsibility and foresight."

The Conference recognized the urgent need for rapid and widespread action to stem the growing loss of irreplaceable germ plasm. The proceedings of this Conference will soon be published by Blackwell Scientific Publications, Ltd., Oxford. It brings together and examines critically what is known about the methodology of exploration, utilization, and conservation of plant germ plasm. More important, the Conference made a series of recommendations to FAO and to member governments. Hopefully these will strengthen efforts to prevent erosion of genetic resources and to accelerate efforts to find, use, and save critical gene resources.

Following one recommendation of the Conference, FAO established a Panel of Experts on Forest Gene Resources. The panel has 10 members, representing 9 nations or regional organizations. Its first meeting was held in Rome on October 21-25, 1968. I had the honor to be elected chairman of this panel. We hope that our efforts will help in planning and coordinating international efforts to explore, utilize, and conserve the gene resources of forest trees.

To this end the panel's report[1] summarizes recent and current activities and recommends both short- and long-term programs for FAO. For the 1970/71 biennium, we recommended that $40,000 should be made available under FAO's regular program for seed procurement. It would be used to

[1] *"Report of the First Session of the FAO Panel of Experts on Forest Gene Resources," Food and Agriculture Organization of the United Nations, Rome, 1969, 44 p.*

augment the efforts of IUFRO and of three research institutes in Mexico, Australia, and the United Kingdom. This represents a considerable increase over the $10,000 to $15,000 contributed by FAO in each of the past two biennia to augment the eucalyptus seed collection of the Forest Research Institute at Canberra, Australia. Further, we recommended that this program should be increased to a level of $140,000 per biennium starting in 1972/73. Numerous other technical and policy recommendations were made to FAO, to IUFRO, and to member governments. Details can be found in the panel's report.

FAO also authorizes and supports several regional forestry commissions. These foster cooperation among member governments. The United States is a member of the North American, Latin American, and Asia-Pacific Forestry Commissions. Other Commissions are organized for Europe, the Meditteranean Region, and the Near East. These Commissions can actively support international programs to exchange and conserve forest tree breeding materials.

A case in point is the Working Party on Forest Tree Improvement of the North American Forestry Commission. The Working Party members from Canada, the United States and Mexico are arranging for needed seed collections, for comparable plant quarantine regulations, and for growing and testing of exotic material in other countries. Information on this Commission and its Working Group may be obtained from the Forest Service, Washington, D.C. 20250.

FAO has other organizational affiliations that can be of assistance in arranging for the collection, exchange, and conservation of forest tree germ plasm. A Committee for Coordination of Mediterranean Forestry Research has been active in such work. The Committee on Tropical Forestry might give similar help where a need exists.

The International Poplar Commission has been very active in supporting the exchange and conservation of poplar germ plasm in the past. This is a Technical Commission of FAO with a Secretariat in Rome. Recently this Commission, through the Poplar Council of America, collected and distributed seed of *Populus deltoides* Bartr. This Commission, through its member nations, reaches most people interested in the breeding of poplars and related species.

Of course, the staff of FAO's Division of Forestry and Forest Industries helps in exchange and conservation of forest tree germ plasm. One Section serves as a clearing house for information on national and international seed collection efforts. Other staff members coordinate and provide technical assistance to forestry projects supported by the United Nations Development Programme. They also are in the process of revising their "World Directory of Forest and Forest Products Institutions." The revised "FAO Forest Tree Seed Directory" is scheduled for publication in 1972/73. Both of these publications are extremely valuable to anyone interested in acquiring forest tree germ plasm or in arranging for the growing of experimental plant materials in another country.

The United Nations Development Programmes (UNDP) supports a number of Special Fund and Technical Assistance projects dealing with forestry. Some deal specifically with tree breeding. Of course, the number and location of these projects constantly changes. Only by contacting FAO can one determine the possibilities of using one of these projects to assist in obtaining seed or other materials. As a result of past UNDP

projects, Forestry Research Institutes have been strengthened in Turkey, Tunisa, Costa Rica, China (Taiwan), Pakistan, Malaysia, and other countries. These Institutes have been and probably will continue to be important sources for obtaining forest tree germ plasm.

IUFRO

Section 22 of IUFRO serves the member organizations with activities involving "the study of forest plants," particularly with forest tree breeding. Several Working Groups of this Section are actively engaged in exchanging, testing, and conserving forest tree germ plasm. Only two Working Groups will be mentioned here.

The Working Group on the Collection of Seed for International Provenance Trials is under the direction of Mr. Helmuth Barner at Humlebaek, Denmark. This Working Group brings together the research organizations desiring seed for provenance trials. The reason for the formation of the Working Group was the extensive international interest to acquire seeds of conifers growing along the Pacific Coast of Western North America. Since the Working Group was formed in 1965, annual collection expeditions have been made to Canada and the United States. As of July 1969, 48 institutions in 26 countries have received 1720 samples of Douglas-fir and 1217 samples of lodgepole and shore pines. Collections of Sitka spruce, ponderosa pine, and associated species are also underway. This Working Group, having developed a unique procedure for international financing of seed collections, might be able to assist in acquiring seeds of desired species from Europe and Asia.

Another Working Group is concerned with the coordination of international provenance research. This Working Group is under Mr. Pierre Bouvarel at Nancy, France. It has two primary functions: the first is to bring together information on existing provenance trials for those who desire access to people knowledgeable about tests already made on species that concern them; the second is to coordinate provenance trials now being established with seed collected by Barner's Working Group and by others.

OTHER INTERNATIONAL ORGANIZATIONS

The International Biological Programme has a strong interest in promoting international cooperation through exchanges of plant materials and evaluation of plant resources. These activities are carried on under Section UM concerned with the Use and Management of Biological Resources. International programs, having a broad interest and requiring international cooperation, can be proposed to each nation's IBP committee for recognition and support.

The International Union for the Conservation of Nature (IUCN) is primarily concerned with the preservation of natural resources. Its Survival Service compiles lists of endangered species and engenders support for protection. Any species, provenances, or populations of forest trees that are threatened with extinction or loss of valuable gene resources through the actions of man should be called to the attention of this organization. Efforts to preserve threatened species might be supported by the IUCN.

The International Union of Societies of Forestry is having its organization meeting this week in Washington, D.C. This organization in the future should provide a communication link for tree breeders to reach those interested in forestry and probably also those interested in tree breeding in other countires. This channel may be particularly valuable if a breeder does not know anyone concerned with forestry in a foreign country.

Several other multi-national organizations exist and can be useful in arranging for the exchange of forest tree breeding materials. Perhaps the most active of these organizations has been the East African Agriculture and Forestry Research Organization (EAAFRO) at Muguga, Kenya. Another that is expressing increasing interest in this topic is the Latin American Forest Research Institute at Merida, Venezuela.

NATIONAL ACTIVITIES

Many nations participate actively in collecting, exchanging, and conserving forest germ plasm. To list all would be impossible, and certainly many would be overlooked. However, several are worthy of metnion. These are the countries which have generously collected their own seeds and provided them at little or no cost. Australia's Forest Research Institute at Canberra has systematically collected seed representing many species and provenances of eucalyptus that are in most demand around the world. Mexico's National Institute for Forestry Investigations at Mexico City has been doing the same for pines and other conifers. The U. S. Forest Service has distributed more than 5,600 samples of seed through its exchange program since 1955.

Several nations participate in overseas development programs from which seed exchanges have been forthcoming. Examples of some of these are the Thai-Danish Teak Improvement Centre which started operations in Thailand early in 1965 and a Thai-Danish Pine Improvement Centre which recently started. A new Danish-FAO Tree Seed Centre at Humlebaek will specialize in seed procurement in southeast Asia. The French Centre National de Recherches Forestieres has cooperated in collections of seed from Turkey, and the Centre Technique Forestier Tropical is developing provenance trials with several countries in western Africa. Norwegian bilaterial aid and EAAFRO have joined forces to explore and collect seed in the Caribbean. The United Kingdom overseas aid program is sponsoring seed collections by the Commonwealth Forestry Institute at Oxford. This program concentrates on the fast-growing tropical hardwoods and conifers of concern to Commonwealth countries.

A slightly different program is supported by the United States under Public Law 480. Administration is by the Agriculture Research Service in the Department of Agriculture. Under this program, excess currencies are used to support forestry research in certain countries. Breeding programs, seed collections, and conservation of forest tree germ plasm are supported. Under certain circumstances, PL 480 projects can be helpful in providing seed that is needed for research in this country.

Certainly the great contributions to international cooperation by individual research institutions and scientists cannot be overlooked. An enormous volume of seed is exchanged strictly on a cooperative basis in order to further research programs of both the sender and the receiver. A new listing of the workers in forest tree breeding around the world has

just been compiled by Dr. Hans Nienstaedt at Rhinelander, Wisconsin. This will be an extremely valuable directory for those who desire to exchange seed on a personal basis with scientists in other countries.

CONSERVING FOREST TREE GERM PLASM

Greater attention has been given here to the problems of exchanging germ plasm than to the topic of conserving forest tree germ plasm. This reflects the fact that conservation of germ plasm for forest trees is of less concern than it is for crop plants. Forest trees have a comparatively long life span and a long reproductive period. Relatively few tree species are in danger of extinction or of genetic change. In fact, the FAO Panel of Experts lists only the following as endangered:

Abies nebrodensis (Lojacono-Pojero) Mattei
Araucaria angustifolia (Bertoloni) O. Kuntze
Aucoumea klaineana Pierre (coastal provenances)
Cupressus depreziana Camus
Pinus caribaea var. *bahamensis* Barrett & Golfari (Great Abaco, Andros, Grand Bahama)
P. eldarica Medw. (a variant of *P. brutia* Ten.)
P. maximartinezii Rzedowski
P. merkusii Jungh. and de Vriese (Sumatran provenances)
P. occidentalis Sw. (Dominican Republic and eastern Cuba)

Of greater concern may be the problem of genetic change due to man's disgenic practices. Where conservation of the germ plasm of a species or provenance is important, we face several problems. Very often the countries having threatened populations are unconcerned. Even if the problem is recognized, solutions often are difficult. Conservation nearly always requires additional funding. Legal sanctions usually are required to prevent continued exploitation or desecration. Ethnic traditions, such as shifting agriculture in the tropics, usually cannot be changed. The only hope to improve such situations is to identify the endangered species and provenances, to explain the consequences of its loss to responsible authorities, and to exert economic and political pressures to change the factors leading to extinction. Finally, if all preservation efforts fail, then collections must be made to perpetuate the species.

Very often people overlook the very large preservation programs for forest tree material that already exist. National Parks, wilderness and natural areas, and other dedicated forests, where man's influence is excluded, all are effective preserves. Furthermore, normal procedures of harvesting and regenerating forests tend to perpetuate much of the gene pool for forest tree species. Tree breeders and other researchers are planting large areas in species and provenance trials, in arboreta, and for other purposes. All of these serve to conserve the gene pool of our forest tree species so long as conscious selection is not made for or against any particular characteristic.

SUMMARY

Breeding for rust resistance, as for any other characteristic, requires access to a variety of genetic materials. In recent years considerable international interest has developed in the exchange and conservation of germ plasm of forest trees. Obtaining plant materials from other nations or continents can be difficult. Finding reliable seed collectors, paying for collections, political barriers, and restrictive quarantines all may stand between the breeder and the plant material he requires.

International organizations have been extremely helpful in overcoming these obstacles. The Food and Agriculture Organization of the United Nations has played an active role in gathering experts together to highlight the problems, and its commissions, committees, and professional staff work to alleviate them. The International Union of Forestry Research Organizations has active working groups that have been extremely helpful in acquiring seeds and in conducting cooperative breeding. Other international organizations are showing more interest in the problems of tree breeders. National efforts, most notably in Australia, Denmark, Mexico, the United Kingdom, and the United States, have contributed greatly to meeting the needs of forest tree breeders for seeds, pollen, and cuttings.

Conservation of germ plasm is of less concern for forestry than it is for agriculture. Relatively few tree species are in danger of extinction or of dire genetic change. The relatively long life, long reproductive period, and vast areas of native forest trees lessen the need for conservation.

FLOOR DISCUSSION

Panel moderator Bingham withheld discussion on this paper until after a companion panel paper by Dr. Henry D. Gerhold. Floor discussion of both papers will be found there.

INTERNATIONAL RESISTANCE-TESTING OF WHITE PINES: NOW OR LATER?

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ABSTRACT

There is considerable interest in developing ways of testing the resistance of white pines to blister rust and other pests on an international scale. It is timely to discuss how such a testing program may be organized. Its purposes may include searching for resistance genes, studying adaptability of pine genotypes to different environments and pathogenic races, and detecting new pathogens or more virulent strains. Testing can serve various interests of participants, but care must be taken that one objective will not be jeopardized by adding another. A cooperative program that utilizes existing facilities of institutions is proposed. Participating institutions should have sufficient interest, personnel, land, laboratories, and operational funds to assure that the program will be effective. An organizational structure patterned after the U. S. Department of Agriculture's Cooperative Regional Research procedures is suggested. The Committee on Resistance to White Pine Blister Rust, of the International Union of Forest Research Organizations, is the logical group to coordinate the testing. To initiate the program, it is proposed that administrators of institutions that may wish to participate be contacted, and that an organizational meeting be held. Periodic meetings of cooperators will be needed subsequently to coordinate experimental activities. It is hoped that the U.N. Food and Agriculture Organization may be able to support the program in several ways.

INTRODUCTION

As the title implies, I am persuaded that there is a real need for testing on an international scale the resistance of white pines to blister rust and possibly other pests. The pertinent question is "how soon", not "whether" an international testing program should be developed. This opinion is also held by other persons, though I do not know their total number nor all of the lands in which they are located. The size and composition of this gathering, however, is an indication of the substantial interest in pursuing this matter. In these initial discussions we should define the purposes of international testing, describe the facilities that may be needed, and examine the ways and means by which a testing program might be organized.

PURPOSES OF INTERNATIONAL TESTING

Several white pine species already are being tested for resistance against diseases and insects in different regions of the world. It may be assumed, therefore, that there is adequate justification for resistance testing in each of the local regions. What purposes can be served by increased international cooperation and coordination among such tests, beyond the summation of their individual purposes? I can think of four, and there may be still others:

1. To aid in the search for additional sources of resistance genes, by comparing the values of various genotypes exposed to pathogens in different environments.

2. To obtain for various white pine genotypes fundamental information about their breadth of environmental adaptability and their resistance to a spectrum of pathogenic races.

3. To determine the adaptation and resistance of provenances or improved varieties in regions other than those for which they were selected originally.

4. To utilize test plantings as an early warning system for detecting more virulent strains or serious new pathogens.

It should also be noted that resistance test plantings may be utilized for other pursuits closely related to resistance breeding, such as provenance testing and the preservation of gene resources.

These purposes illustrate that persons who might wish to participate in an international testing program would do so for different reasons. The reasons of one might not even be fully understood by another. An industrial silviculturist in northern Italy may want to compare the relative merits of various white pine varieties or provenances available from Europe, North America, and Asia. A university pathologist in Sweden may want to compare biochemicals extracted from *Cronartium* races interacting with various host genotypes. A government tree breeder in eastern Canada may wish to estimate genetic variances of weevil resistance that apply to a broad region including northeastern United States. The diversity of professions, employers, host species, and pathogens indicated by these examples must be taken into account when plans are developed for facilities and particular experiments. This does not mean that each facility and each experiment can serve all objectives. Facilities and experiments should be efficient in producing as much useful information as possible, but care must be taken that one objective will not be jeopardized by adding another.

DESCRIPTION OF TESTING FACILITIES

It would be gratifying if it were possible to build, staff, and operate entirely new resistance testing facilities designed to ideal standards. But I do not know of any single source from which sufficient finances could be obtained. To be more realistic, we should limit our considerations to the capabilities of existing institutions. What attributes should they have in order to participate effectively in international resistance testing? Some of the more important ones include:

1. Sufficient economic or scientific interest in the host and at least one of its pathogens to justify the allocation of personnel, land, laboratories, and funds from time to time.

2. At least one scientist who would have primary interest and responsibility in the project, plus supporting personnel all of whom together are well qualified to carry out required experimental procedures.

3. A nursery for growing seedlings and, in some cases, for artificial exposures to pathogens.

4. Land for experimental plantings that is in stable ownership, representative of sites on which the species is to be grown after testing, and conveniently located for making periodic measurements.

5. Any laboratory space, equipment, or supplies that may be required for analyzing results.

6. Funds for the above items, and for maintenance costs, field measurements, and travel to meetings needed for planning and coordination.

Because of the various procedures involved in resistance testing, cooperation will be needed among personnel with different abilities. The procedures include breeding and propagation of trees; culture of fungal, insect, and possibly bacterial and viral pathogens; recognition and measurement of disease symptoms; protection against spread of pathogens; experimental design and analysis; genetic interpretation of results; and silvicultural and economic evaluation of phenotypic variation. The activities should be coordinated by a person or committee that understands all facets of the work, and that enjoys the confidence of those who can provide the resources.

ORGANIZATION OF THE TESTING PROGRAM

All of the elements required for an international resistance testing program for white pines are already in existence, though not necessarily at optimum levels. Considerable time, effort, and persuasion may be necessary, moreover, to find the common or compatible interests shared by potential participants, to develop detailed objectives and procedures, and to arrange for required resources. Because of the magnitude and duration of the program, I believe that an organizational structure with clearly defined responsibilities of its members is a necessity. I further suggest that it be developed through existing organizations, and that it be kept as simple and informal as possible. The international provenance tests of the International Union of Forest Research Organizations (IUFRO) and the Regional Research Projects of the U. S. Agricultural Experiment Stations have provided useful experiences and guidelines for conducting cooperative research.

With these considerations in mind, I would suggest that the following steps be taken in order to organize the testing program:

1. The IUFRO Committee on Resistance to White Pine Blister Rust has already started to consider an international testing program, and it is the logical group to coordinate its operations. The scope of the program needs to be clearly defined in terms of tree species, pathogens, geographic regions, and test objectives. Considerable progress along these

lines doubtless will be realized at this meeting. At a later date potential participants should be invited to a 2- or 3-day organizational meeting, which might be held at the next IUFRO Congress.

2. At the organizational meeting, procedures for coordinating the work should be adopted, possibly using the U. S. Department of Agriculture's "Manual of Procedures for Cooperative Regional Research" as a model. Then tentative outlines of individual experiments should be drawn up including title, objectives, procedures, and participants.

3. Administrators of institutions that may wish to participate in the program should be contacted, preferably both before and again after the organizational meeting. The reasons are to acquaint them with the program, to learn the nature of their interests, and to negotiate agreements on the terms of their support.

4. Periodic meetings of all cooperators should be scheduled to assure adequate funding, continued progress, occasional revision of the program, and timely publication of results. It would also be useful to invite representatives of the U. N. Food and Agriculture Organization (FAO) and related IUFRO groups, e.g., Section 24 Forest Protection, and the Section 22 Working Group on Provenance Testing.

5. The sponsorship and support of FAO should be sought for assistance with monetary and diplomatic problems. Three special needs come to mind. First, it would be most helpful if FAO could temporarily provide a specialist in resistance breeding to make personal visits to institutions that may wish to participate (see Item 3). As an emissary representing the sponsors and the organizers, he could assist administrators in reaching decisions about their participation. Without the impetus given by personal visits, it is questionable whether Committee members would have enough time and energy to overcome the various types of inertia that could prevent the program from getting underway. Secondly, some means of obtaining reimbursement for the cooperators' travel expenses to Committee meetings (Item 4) must be found. It is very difficult, often impossible, to obtain travel funds for international working meetings through regular channels. Finally, it will be necessary to increase the wind pollinated seed collection and controlled pollination work of some cooperators so that there will be enough seeds for other participants. It may be advisable to ask FAO to administer a special fund that would support breeding or other activities carried out by one cooperator for others, the funds to be supplied by participating institutions.

CONCLUSION

In conclusion, I feel that we are considering investment in a very ambitious program, but one that can succeed and can pay valuable dividends. My suggestions for organizing the program are offered in order to stimulate discussion of these and other alternatives, so that the best means of proceeding may be found. I can see no good reason for delay. If we don't start planning for international resistance testing facilities *now*, they will not materialize by themselves *later*.

FLOOR DISCUSSION

(Also covering the preceding paper by Robert Z. Callaham)

CALLAHAM: I'll start the discussion by addressing some remarks to Dr. Gerhold, who presented the other paper involved in this discussion. I can't speak for FAO, but from my association with them I do know their modus operandi, and their limitations. I think I can say with assurance that it will be impossible for them to provide the type of resistance breeding specialist you propose. The FAO has just reviewed their 1970-71 budget, and funds for the third (tree-breeding, or forest geneticist) officer in their Section were not provided. They should establish this sort of overall position before adding or working on a specific problem like you suggest. Such specialist positions have low priority at present. They would seem to be impossible to finance within the decade. So I think you'll have to look elsewhere than FAO. I agree that there is need for such a coordinating specialist, but I feel his support will have to come from the generosity of a government, individual organization, or foundation that may consider the problem sufficiently important. Helmuth Barner has received support for his working group's tree seed collection activities from the Karlsberg Foundation. Perhaps the support you need could be provided by a foundation. In another vein, I don't think we are ever going to get other than local support for travel to committee meetings. In a cooperative program participating organizations must go all the way in supporting and obtaining the objectives of their people. If this were part of a U.S.D.A. program, travel funding for U.S.D.A. people might be possible. Internationally we lack an organization to support travel. Lastly, I want to make the point that under certain circumstances FAO can bank pooled monies and pay in foreign currencies. For instance, A has expertise and facilities wanted for testing, or materials wanted for exchange, but cannot finance their operation, or collection. B, C and D are willing to pay for the testing or collection work. B, C and D can give their money to FAO in order to accomplish their goal. International complications disappear.

HAGMAN: Another possibly important source of support is the as yet unmentioned European Plant Protection Organization (EPPO). Recently it has been reorganized and has been able to raise a lot of money from various governmental sources. Also, recently EPPO has shown quite an interest in forest plants, particularly in respect to plant protection laws affecting forest material in international trade. Possibly the approach to EPPO might be that the laws on important diseases of trees cannot be strictly applied without intimate knowledge of the diseases coming from places like international test facilities. Their head office is in Paris. They are cooperating with FAO but are independent as far as their money is concerned. Perhaps Mr. Gremmen or someone else knows more about them than I do.

BORLAUG: There's another group of vehicles, perhaps not useful for forest trees, but you might be interested in how they handle and coordinate their work in agricultural crops. Going back 20 years to when the international rust nurseries were first established, in these nurseries we brought together not only parental types, but any materials breeders in cooperating countries wanted to evaluate in other countries. This project has continued. Results of the international tests are compiled by U.S.D.A. and circulated to all collaborators. If you use them wisely you can pick up another gene to add to the pool with which you're concerned in a given geographic region of the world. Later we attempted to make the

concept useful to breeders beyond just disease resistance. About 11 or 12 years ago we began to work with FAO, initially in a training program preliminary to collaborative work toward coordinating work of international yield nurseries. This program failed because FAO had no one and no funds set aside to coordinate the work. Then we assumed the responsibility at the International Maize and Wheat Improvement Center. Initially this was a joint undertaking of the Rockefeller Foundation and the Mexican Department of Agriculture; it has since been reconstructed into the Center. The yield tests proved to be a wonderful vehicle. Materials were handier and we got useful information on a world-wide basis. First came an international yield nursery for spring wheats--because they fit a temperature range of the area in which we worked, a range not suitable for the winter wheat types. A modest start was made with 25 varieties representative of the main spring wheat varieties of the main world wheat regions. We always included some of our own best experimental lines and we solicited experimental lines from other countries but at first didn't get any. Now, because of growing use by breeders everywhere, we always have these new, experimental lines; in fact, we've doubled the size of our nursery. All seed stocks are grown in Mexico from imported seed. At present a yield nursery planting involves 80 uniform sets of seed, sent to 80 collaborators all over the world. There's a demand for 150 sets, but we can't supply them. Instead we supply strictly experimental materials for about 20 "screening" nurseries known to be fairly uniform for yield. From the main yield nurseries we get disease information, dates of flowering and maturity, heights, degree of lodging and a lot of other miscellaneous data that are compiled in a computerized annual report. The screening nursery is a much simpler thing, but it's the one that really gives you the new, basic information. Very early in the program you're able to identify unusual, and potentially useful lines. Good yields in one locality identify ecotypes or provenances adapted to that local site. You find some provenances broadly adapted to a wide range of conditions holding on irrigated lands, dry lands, fertilized or unfertilized lands and to a wide range of disease conditions. At present we find most of these unusual lines in our basic gene pool in Mexico--but the system hasn't been functioning too long. I have long since learned that if there is a full-time coordinator to handle, compile and distribute these data to collaborators that international participation will increase 2 to 5 times the amount you can handle. Thus I say to both of you (Gerhold and Bingham), God bless you for your attempts to set up a similar facility for international testing of white pines and white pine blister rust resistance. Don't let the organization become too bureaucratic so that it dominats and stifles the ultimate effort. Make it simple.

BINGHAM: Dr. Borlaug, these wheat yield and screening nurseries programs that are carried on by the International Maize and Wheat Improvement Center, what was the initial source of financing?

BORLAUG: At the present time we are working with wheat, but in Latin America we are now following up with maize (corn) and developing a smaller but similar potato program. Our financing came from the Rockefeller Foundation. Here, I think you may be bypassing some good opportunities in working with certain foundations. Possibly you have explored these possibilities but I'd like to talk with you about this sometime.

BINGHAM: Thank you. The Committee on (resistance to) White Pine Blister Rust would certainly welcome your attendance at their meetings of the next few days.

BORLAUG: Somewhere I heard Dr. Callaham mention Public Law 480 funds. I think that from P.L. 480 projects in both India and Pakistan there is excellent opportunity for getting support for blister rust resistance testing there. I would propose that the first contact there be to the country's Director for P.L. 480 programs. Go to the Director to get approval there, rather than the other way around. Is our Indian friend Dr. Kedharnath here? Can you tell us whether there is any P.L. 480 funds going into this blister rust program at the present time?

KEDHARNATH: No.

CALLAHAM: The Forest Service has a man going to both countries in October for this purpose. But tell us what you think about the need for a coordinator.

BORLAUG: I think you must have such a person.

CALLAHAM: Yes, I understood the ultimate need. But with all the travel involved for the coordinator, and the reoccurring need for collaborators to meet together in one place, I'm worried. The coordinator and related travel would represent a big expense to which there would be resistance. Could initial coordination be established by mail?

BORLAUG: In the beginning, yes, but I think that to have really strong coordination personal contacts are necessary. At the Center in Mexico, our original contacts were through young trainees. Over the last 10 years we have brought perhaps a hundred of these young scientists to Mexico, in our wheat program alone. Part of this trainee program was financed by FAO fellowships part by the Rockefeller Foundation. You simply convince people--to prevent bottlenecks at top governmental levels--of the benefits coming to them from their part in the international collaboration. Then, because it's two-way informational exchange, with useful data coming in to them, collaboration is wonderful. A central meeting every 3 to 5 years is necessary. We had one last year in Pakistan, sponsored by FAO and Rockefeller, where collaborators were brought back together. There we went over these very problems, and how to improve collaboration. Everybody was asked to participate, and on some points they really criticized the program. From the recurring, if not annual contact you can build up a very effective vehicle. On another point, I think you're right in this white pine program in taking the plant to the rust. I don't think you should spend all your time and budget determining how many races of *Cronartium ribicola* are present locally. By taking white pines to the centers of rust origin you see immediately that the rust varies. Thus the international testing tells you, indirectly, which materials in your own gene pool are likely to be best. I have no doubts about this process, and you don't need a lot of highfalutin data to prove this. The plants will talk to you if you'll listen, and if you give them the chance to express their likes and dislikes to pathogens to which they may be subjected.

BINGHAM: Perhaps, at present, we still lack a lot of the basic technology needed to assay material in international disease gardens, but this will develop only when we begin to subject new materials to the different races, preferably near host:parasite gene centers.

GERHOLD: On behalf of the IUFRO Working Group on Genetic Resistance to Forest Insects and Diseases, I had previously contacted the Rockefeller Foundation and the Ford Foundation. Replies from both Foundations were

essentially the same--that their emphasis for the present is on food rather than fiber. Perhaps I didn't reach the right people.

BORLAUG: I think you should have another try at it.

GERHOLD: A coordinator of international tests, whether he were financed by FAO or by other means, could really accomplish quite a lot in a month or two by visiting several key institutions. Some institutions or organizations occasionally have surplus funds that can be applied to timely requests. Such funds might be of temporary use to get a project started.

CALLAHAM: Perhaps if not through FAO, through the United Nations Development Program (UNDP) special funds project or their technical assistance program. Here it might be possible to finance one person for making a one-shot coordination visit, but to establish long-term continuity of visitations would be almost impossible. I think the best way to assure long-range coordination is to get, if not a foundation, some benevolent government to finance this. This would have to be a government so vitally concerned with the white pine blister rust problem that they would support the long-range program.

GERHOLD: One other point in respect to securing support for international travel. Meetings of the White Pine Blister Rust Committee here have indicated that some means of reimbursement for travel must be found if the Committee is to function. After international testing centers are organized supporting institutions may begin to recognize the benefits, and they would then be likely to consider travel expenditures more favorably.

PANEL III

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THE THEORETICAL BASIS OF RUST RESISTANCE TESTING--CONCEPT OF GENETIC GAIN IN BREEDING RESISTANT TREES

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ABSTRACT

Co-evolution of host and parasite under exclusively natural selection leads to an equilibrium with specific genetic features on both sides. A genetic equilibrium based on gene-for-gene relationships is not likely to be expected if the host is a long-lived tree species and the parasite a fungus fatal to infected trees. Host-parasite systems of this type might be equilibrated predominantly by means of polygenic systems on both sides. Prediction of genetic gain of selection for higher resistance in such situations involves the risk of biases resulting from counterselection in the parasite population. Chances for predicting genetic gain of selection in the host are better if the parasite has only recently been introduced and the genetic properties of both populations tend to either the establishment of a genetic equilibrium or the extinction of the parasite by complete resistance of some host genotypes.

It is most likely that newly-"recruited" genotypes of the host with high or complete resistance are bearers of specific gene combinations, and that genetic variance of resistance in such cases is largely non-additive (epistatic). Mass selection or related breeding procedures are of limited value here.

Correlation of resistance in different stages of development or in different ages is of vital importance for the reliability of estimates of genetic gain which are mostly based on results from experiments with younger plants.

Some discussion is given on how to describe the problem in a general way and how both theoretical and experimental results from biometrical genetics can help to meet the main difficulties. The overall conclusion is that more research is required before a satisfactory and sufficiently general model can be presented.

INTRODUCTION

Both animal and plant breeders and particularly breeders of long-lived species have to bring their breeding programs close to an economic

optimum. Among the information needed for planning an optimal breeding program, genetic variances and heritabilites of characters under selection are of utmost importance. Estimates of these parameters serve as a base for calculating genetic gains to be expected from different breeding procedures where mass selection or related procedures are to be planned, where the characters in question are of the typical quantitative type, and where the population size is sufficiently large in each generation of selection to eliminate random effects of sampling. It seems reasonable, therefore, to try to extend the concept of genetic gain to the field of resistance breeding, as has been done by Bingham, Squillace, and Wright (1960) for resistance of western white pine to white pine blister rust, or, at least, to investigate the particular problems to be solved before this can be done.

Breeding for resistance against fungal diseases is by far the most important field of resistance breeding in forest trees. The following discussion is thus restricted to specific problems of this kind of resistance breeding; other problems arising from peculiar features of parasitic organisms other than fungi, like behavioral performance of insects, have been neglected.

GENETIC BACKGROUND OF HOST-PARASITE SYSTEMS

The evolution of parasitism has long been one of the most interesting fields in evolutionary science. It offers examples of extreme specialization of organisms such as the adaption of metabolic cycles of parasites to the performance of one or more host species. Host species, on the other hand, are often able to evolve special mechanisms enabling them to escape from being parasitized or to eliminate infections.

It seems no longer justifiable to speak of evolution of virulence of parasites without taking into account the simultaneously evolving resistance in the host. Both processes affect each other. Geneticists and evolutionists as well as breeders are stressing this mutual dependence by speaking of co-evolution of parasitism or of evolution of host-parasite systems. Genetic interactions between host and parasite are often evident within short periods. When selecting for higher resistance the breeder tries to change such a system by favoring the host. He might either work on a host-parasite system that has reached an equilibrium state or on a disequilibrated one.

Much of the theoretical and experimental work on resistance breeding has been done on host-parasite systems characterized as gene-for-gene systems (Flor, 1955). Mode (1958, 1961) was able to define some special cases where stable equilibria can be reached if the host population possesses a set of genes for resistance (R-genes) and the population of the parasitic species is able to activate a set of genes for virulence (V-genes), each of them overcoming resistance reactions of one or several R-genes. Person (1966, 1967) was able to verify one of the stable equilibria predicted by Mode (1958) in a wheat:wheat-rust gene-for-gene system.

Gene-for-gene systems with many genes on both sides are not likely in host-parasite systems where the host is a tree species and the parasite a fungus. Generation intervals are too different, favoring the parasite that is often able to produce more than a hundred generations while the host is producing only one generation (Hattemer, 1967). The same is

probably true for similar systems involving a space component (Pimentel, Nagel, and Madden, 1963).

The findings of some forest tree breeders of resistance reactions apparently inherited in a simple Mendelian way (Søegaard, 1966, for example) do not contradict our expectations about the genetic background of resistance of tree species against fungal diseases in equilibrium systems. But they might indicate the existence of different types of host-parasite relations or of resistance barriers in one species which might be lacking in a different but closely related species. We should distinguish here between fatal diseases and others that rarely or never are fatal to the infected host; we should further consider the various ecological situations of host-parasite systems.

Genes for resistance from a related host species might be particularly useful for a breeder who is dealing with evolving host-parasite systems like in the case of a newly introduced parasite. The genetical side of host-parasite systems has been described by Pimentel (1968) as a genetic feedback system. This is probably the most general model for dealing with mutual effects of genetic changes in both populations. But genetic feedback means no more than a general description of the genetic interplay of host and parasite. It seems, therefore, to be necessary to specify some situations where this genetic feedback can work. The gene-for-gene system represents only one of them. The general model of genetic feedback described also all the other systems operating between hosts and parasites having genetic equilibria, and where permanent survival of both populations is possible as a consequence.

We have to restrict ourselves here to discussion of 2 specific cases. In one of them, resistance behaves like a typical quantitative character in the sense of quantitative genetics, at least within a certain range. In the other, resistance behaves like a threshold character with a more or less narrow physiological or biochemical range, acting as a kind of threshold above which resistance (or below which susceptibility) is absolute for all genotypes. Selection might lead in both cases either to absolutely resistant populations, to better resistance, or to less resistance, the last two reactions being the results of changing the genetic equilibrium points.

MAIN ASSUMPTIONS TO BE MADE WHEN THE CONCEPT OF HERITABILITY AND GENETIC GAIN ARE TO BE APPLIED IN RESISTANCE BREEDING

The outcome of mass selection or of related procedures over a few generations of selection can often be predicted by using the well known equation for "genetic gain" or "response to selection", $R = h_e^2 S$. R stands for response to selection and S for the difference between the mean of the unselected population and the population of selected "superior" individuals. h_e^2 is the ratio of additive-genetic variance and total phenotypic variance or its equivalent in an experiment. This ratio at the same time is a measure of regression of progenies on parents which makes it an estimate of response to selection for a selection experiment with a given S.

But R can be estimated accurately in this way only if:

1. There is no contraselection on the side of the parasite,

2. There are no genotype-environment interactions, i.e., no dependence of host-parasite relations on the environment,

3. There is a strong correlation of character expression in different stages of development, i.e., no dependence of resistance on host age.

Tree breeders might decide whether or not these assumptions hold in a given case. It is of course possible to verify this experimentally, but it takes time and should be combined with basic experiments on the genetical, physiological, and biochemical background of resistance and virulence, and the different opportunities of the genetic systems of both host and parasite to make use of genetic variability.

If resistance is inherited by major genes and if identification of bearers of genes for resistance is possible with sufficient reliability, the older gene-frequency approach from population genetics might be preferred. The proportion of resistant individuals expected after one generation of selection can be easily calculated in such simple cases if it is known whether R-genes are dominant, partially dominant, intermediate, or recessive. The degree of penetrance and expressivity can also be accounted for. But the great unknown quantity here is the probability of emergence of new V-genes on the side of the parasite. This cannot be accounted for in a reasonable way because it is a rare and unpredictable event.

Genetic gain in a threshold model can also be calculated as usual for purposes of resistance breeding. The same assumptions are to be made as in the case of typical quantitative variation of the character "resistance". But the problem here is dependence of threshold values on the environment and/or age rather than dependence of resistance on both complexes. One of the main difficulties still to be solved arises from the fact that we might expect threshold ranges rather than threshold values. This means that resistance against a variety of genotypes of the parasite might fall in a more or less narrow part of the total range of variation of the character that determines the threshold. There might also be a chance for the environment to change the threshold range.

Resistance is most likely to be a threshold character if its base is of the biochemical kind, for concentration of a biochemical agent is related to its toxicity. One could easily construct quantitative-genetic models making one or more major genes on the host side responsible for the production of a toxic substance, the concentration of which is varied by modifiers. Virulence in the parasite can be inherited in the same or a similar way. This model would easily account for a situation where resistance is gradual in a certain range and absolute above a threshold point. Mülder (1953) has shown that situations similar to this are given in both resistance of white pines to *Cronartium ribicola* J.C. Fisch. ex Rabenh. and of Scotch pine to *Peridermium pini* (Pers.) Lev.

MAIN ASSUMPTIONS TO BE MADE IF COMBINING ABILITY IN THE GENERAL SENSE IS TO BE USED

Resistance can also be caused by epistatic gene effects, as, for instance, Wright (1956) already has pointed out. Only a small portion of genetic gain is due to epistatic components of genetic variance when mass selection is applied, and only components of the additive x additive type can be used in mass selection or related procedures. Breeding

schemes like reciprocal recurrent selection are to be preferred in such cases.

There seems to be hardly a chance for epistatic gene effects to play a major role in equilibrium systems of host and parasite, because epistatic equilibria are possible only in exceptional cases. But the reverse situation can be given if the parasite has been newly introduced or breeding for resistance in a territory that has been newly opened for the host. Both situations in principle are similar to what in population genetics has been circumscribed by the terms, "use of preadapted genotypes" or "use of recruited genotypes" (see Spiess, 1968, for summary and references).

Recruitment of genotypes means the emergence of hitherto unknown qualities of some--often very rare--genotypes of a population after the population has been exposed to a rather drastic environmental stress. Preadaptation means that some of these genotypes are better adapted to the new environment; they might, for instance, be more resistance to a newly introduced disease. It is therefore the special case of recruitment where useful genotypes have been recruited by nature or by the breeder. Epistatic gene effects might be one of the major causes of preadaption, as pointed out by Wright (1956). Crosses between preadapted individuals thus need not necessarily result in resistant progenies. But it should be possible to find parents of high specific combining ability among the group of preadapted genotypes or to develop appropriate crossing designs for the use of this type of genetic variation.

Bingham *et al.* (1969) could show that the proportion of nonadditive genetic variance of the total genetic variance increases with intensity of infection (proportion of infected individuals). This is in full agreement with our expectation. As long as the infection rate is low, small differences in phenology might be of some value in increasing resistance. Under normal circumstances this means possessing characters adaptive to environmental factors rather than resistance to a newly introduced parasite. The genetic variances of such characters are predominantly of the additive type. But other preadapted types must be "recruited" from the population if the probability of infection increases. Under such conditions the only truly resistant genotypes might be those which normally have inferior selective values or might even belong to the genetic load of the host population. This is a troublesome case for the breeder since epistatic genetic variance is difficult to assess in the common type of experiments like the diallel cross. Kearsey and Jinks (1968) have given some new ideas on how to proceed in such cases. But much more work should be done or must be done before breeders are able to make use of epistatic genetic variance in a sufficiently simple way.

Vogl, Schönbach,and Haedicke (1968) give an example of preadaptation in resistance to an abiotic damage. Different provenances of Japanese larch proved to be of different resistance to air pollution, the degree of resistance being correlated to some unknown or only partly known adaptation to the climate in the places of origin. This is probably an example of preadaption of the type mentioned first.

GENETIC CORRELATIONS IN RESISTANCE BREEDING

Resistance is not what could be called a basic character (if there are basic characters at all, except nucleotide sequences in DNA or sequences of amino acids in polypeptides, etc.). It is a byproduct of some anatomical, physiological, or biochemical feature of the host organism leading to disturbance of a host-parasite relation (see Williams, 1964, for a review for plant breeders). This means that there must be genetic correlations between resistance and other characters. These correlations can be treated as any other genetic correlations, i.e., correlations of breeding values (Falcolner, 1964). But it seems very difficult to find solutions for more complicated situations, because the theory of genetic correlations is almost exclusively a theory of correlations between breeding values of two or more characters, at least in its parts that are of some use to the breeder. Naturally there must be other causes for genetic correlations besides additive effects of genes on several characters.

A breeder of long-lived organisms tests the resistance of his material by laboratory tests or nursery experiments, and in field trials where field resistance and yield of families or strains can be observed for long periods. The more important genetic correlations will be detected easily from comparisons of results of early tests for resistance and results from long-term experiments.

One of the most important genetic correlations is correlation of resistance in different stages of development and/or in different environments. They can both be treated in the usual way, again if correlations of breeding values are to be accounted for. The forest tree breeder seems to be particularly interested in genetic correlation of seedling resistance and resistance of mature trees. In fact, selection for white pine blister rust resistance has widely been selection of resistant seedlings where some degree of resistance during the complete life cycle is the economic objective. Seedling selection or selection of young plants from vegetatively propagated selected trees seems to be the best approach. Haack (1914) inoculated mature trees when trying to evaluate the heritable portion of resistance of *Pinus silvestris* L. against *Peridermium pini* in mature stands. A high proportion of his inoculations were successful if the tree was already infected, but only few or none were successful if the tree did not show spontaneous infections. This method could serve as an excellent means for early evaluation of correlations of resistance in seedlings and mature trees. It also gives some indication of the degree of resistance since Haack found that the proportion of successful inoculations in a tree was correlated with the number of spontaneous infections in that tree.

Mülder (1952, 1953, 1954, 1955) has made some comparisons of the course of infection of a stand with increasing age. He found quite different developments in stands of eastern white pine attacked by *Cronartium ribicola* and stands of Scotch pine infected by *Peridermium pini*, both fungi being closely related and very similar in reproductive behavior. The average degree of resistance was much higher, of course, in Scotch pine, the host-parasite system being much older here and having probably reached some kind of equilibrium. But it is interesting to see how the proportion of infected trees in both cases increases with age. This is probably not only a consequence of a better chance for infection during a longer period--Mülder found more infections in trees with larger crowns and we cannot outrule this factor completely--but certainly also a consequence of the threshold of resistance changing in time. It could

also be affected by selection in the population of parasites. Much more work is needed on the ecological, physiological, and genetical background of this trend in resistance; but there can hardly be any doubt that it exists. We should look upon results of laboratory tests or nursery experiments from a different angle. The character selected for in early tests, i.e., resistance of seedlings or small plants after vegetative propagation, should be correlated with the probability for infection during the complete life cycle of the tree, the family, or the strain, at least up to an age where it is of economic importance. Genetic gain of indirect selection, which means selection for a character that is easy to assess and correlated with one or more characters of economic importance but difficult to assess, means genetic gain in the probability to escape infection up to an age where infection is no longer important from an economic point of view. This probability, referring to a larger proportion of individuals of the family or strain, must be put into the equation for genetic gain from indirect selection as given by Falconer (1964).

Calculations of genetic gain from indirect selection might be further complicated in our case by genotype-environment interactions and by incomplete control of environmental factors in laboratory tests or nursery experiments. Resistance in any stage of development can be subjected to interactions of this type. Bingham (1968 and these proceedings) has shown pronounced effects of seed bed environment on proportion of plants infected by white pine blister rust.

DISCUSSION

The common base of all methods for estimating quantitative-genetic parameters of a population are covariances between relatives. There are no principal differences between procedures to be applied to different characters, the mathematical side having been discussed thoroughly in textbooks of quantitative genetics and breeding. Therefore we have concentrated here on some of the major problems of model-building resulting from the genetics of host-parasite relations. It will certainly never be possible to put all the parameters needed for complete accounting into one biometrical model. But we might be able to refine our models to make predictions more reliable if we are aware of the biological peculiarities of host-parasite systems and of possible fallacies which might result from applying oversimplified models.

There is certainly a good chance for employing the concept of genetic gain also in breeding for resistance if the breeder can be sure his model fits the particular case he is working on. The main additional assumptions to be made if predictions of genetic gain shall be calculated for resistance have been given above.

The breeder should try to verify whether these assumptions really hold by using evidence from both observations in the forest and basic experiments on physiological and genetical features which might be relevant to understanding the host-parasite system and hence to understanding the background of resistance which he wants to establish or to increase quantitatively in the host population.

This combination of field and laboratory work seems to be the best approach to all problems of ecological genetics (Ford, 1964). Results from planned experiments following the rules in quantitative genetics can

be of utmost importance for designing a resistance breeding program if they are seen in the general framework of an ecological-genetical study.

There are also some attempts to introduce into resistance breeding new models from biomathematics like the one of Okabe and Hashigichi (1968). These authors use the theory of games to find the best mixtures of genotypes with respect to resistance. The present author would not propose their particular approach to breeding white pines for blister rust. But it is a good example of the new approaches attempted by research workers all over the world who try to make the outcome of resistance breeding more predictable.

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FLOOR DISCUSSION

BECKER: In the case of the blister rust resistance work of the Intermountain Station here in Moscow, the rust has been present and selection has been proceeding almost 50 years. I would like to ask Dr. Stern, do you think that the blister rust organism itself will change, and therefore do away with genetic advance they have made?

STERN: The white pine is part of the environment of blister rust here, and if you change the environment of an organism it will react genetically--but you can't predict how it will react. There are, of course, cases known where the parasite tended to be less violent in its interaction with the host population. But nothing is known about the genetic background of this, and nothing is known as to which feature of specific genetic combination the host and parasite must have to give this result. To answer correctly we would need to know more about the biological facts relevant to this particular disturbed, disequilibrated host-parasite system.

HATTEMER: I didn't get a clear understanding as to why there must be genetic correlations between any unknown traits that as a by-product bring about resistance--if the phenomenon of recruitment holds.

STERN: Well, if you make things too clear people will think it's no longer scientific. I will try to give you a clearer example. In birch rust, for instance, the phenology of different birch provenances may be quite distinct. Some provenances are early starters, and normally these cease growth quite early in the fall. Other provenances start late but keep growing until the end of October. If birch rust infection occurs early, say before the middle of September, then the late starters have some healthy leaves. Resistance is lower in the early starters where all leaves are infected. This example of the correlation between cessation of growth and resistance is only one of many.

BINGHAM: Dr. Stern, did I misinterpret something you said, that heritability tended to increase as infection became more intense?

STERN: No, I said that the proportion of non-additive genetic variance in the total genetic variance increased, thus that heritability decreased (see this paper; and Table 4, Bingham *et al.*, 1969).

POPE: I'm a wheat breeder for the University of Idaho, not a forester. I don't use genetic models (except to get a clear picture of the generalized binomial expansion) nor read the literature on heritability and genetic gain, but for 20 years now I have been able to handle the resistance. For about 10 years I have used specific resistance genes that worked just like people say they do and collapsed just like people say they do. In 1960 there was superimposed on our wheat populations rather heavy and uniform, natural spore showers of stripe rust (*P. striiformis*) that Miss Fuchs talked about (see Fuchs, these proceedings). At that time my wheat populations were mostly efforts to sample the world sources of resistance for bunt (*Tilletia* spp.), that were mostly the specific gene type. To my surprise we had also sampled a large number of sources for resistance to stripe rust, in a far more sensible manner than we could have been able to do deliberately. In particular I found the usual specific system (or what I assume was, we didn't bother to find out) of dominant genes that gave good resistance located in varieties where people said they were. In addition to this--in what I assume is our uncomplicated race situation--in most of the varieties other people said were susceptible to stripe rust I found from 1 to 3 or more genes for resistance. In the old, hard red spring wheat Marquis, that is mentioned in the literature as being a useful susceptible check, I found 3 resistance genes. In almost every cross I had made for other purposes I found additive interaction for resistance to stripe rust. This follows one of Dr. Stern's models. However, the most striking thing was that some of the spectacular interactions came from wheats that were phenotypically susceptible. It's unfortunate that we must use these descriptive words, because there are only 2 or 3 of them--resistant, susceptible, and immune, with modifying words--while there is a much broader genetic behavioral range. Also, it's a sliding scale. A disease at a given level gives effects you can see with your eyes at one place on the scale. If the disease severity is worse, you slide up the scale and don't see the bottom part of the scale at all. It's my opinion that this is an example of non-specific, multigenic resistance systems, one that is quite widespread and more common than the much better known gene-for-gene relationships. Philosophically I suspect there is a spectrum of different resistance systems that are complimentary to one another. Most wheats with "susceptible" phenotypes turned out to carry genes that contributed to increased resistance in the best propgeny of appropriate crosses.[1] Wheats with "zero" genes for resistance to stripe rust (such as the white spring wheat Lemhi) are rare. As pointed out some of these genes are spectacularly additive with other genes--possibly functioning in a series of chemical reactions where each gene controls one reaction. Without rust there's nothing very useful for the gene, or the complex of genes, to do. I think that in a crude way this situation is comparable to the white pine blister rust, except that there are probably more resistance-genes scattered in wheats. I found these genes in wheats coming from continents such as

[1] *Editors note: See Pope, W. K. 1968. Interaction of minor genes for resistance to stripe rust in wheat, p. 251-257.* In *Proc. 3rd Int. Wheat Genet. Symp., Canberra. 479 p.*

Australia where wheat is a relatively new crop--anyway where wheat hasn't been subjected to stripe rust for the last 100 years. Here there should be neither selection for or against resistance genes. They should float in populations according to the Hardy-Weinberg principle. White pine trees (assuming they haven't been exposed to blister rust for a few thousand years) should contain some similar genes. Of course resistant gene-complexes that provide spectacular resistance might be broken up into single units, imparting little or no resistance separately. I have not watched Bingham's western white pine blister rust resistance work too carefully, nevertheless everything he says points toward multiple-gene resistance. He has some resistant mature trees that produce progeny seedlings only a few of which are resistant; other resistant parents produce more. This suggests multiple-gene heterozygous resistance, and a difference between seedling and mature plant resistance. If the blister rust situation matches that in stripe rust, the main effect is from the total number of genes; that is gene dosage, not dominance. I don't know whether the severe, screening-inoculation of the young white pine seedlings is comparable with the situation in wheat. In my own work wheat plants with good mature plant reistance can be seedling susceptible. Thus I have avoided known seedling resistant wheats on the assumption that resistance was controlled by specific genes that would obscure the more non-specific resistance I was watching. I would suggest that you spend more time looking at trees instead of reviewing the literature and worrying about its implications in trees. Your trees haven't read this literature, and yet you do have wonderful, fairly old, blister-rust-resistant trees out there in the forest. From what you tell me, unless these trees produce a high proportion of resistant seedlings you don't use them. I think this is a colossal mistake. You need more than seedling resistance. Use some trees that have seedling resistance but put all of these trees together in a way they "want" to go together, instead of how you decide they should go together. If you let me warm up I'll add some more commentary on another day.

STERN: This has been precisely what I was referring to--to the two combination effects "general combining ability", contributing to the additive genetic variance, and "specific combining ability" contributing to the non-additive genetic variance, as outlined by Sewall Wright (1956). Wright gave an example (after King, J., 1955. Integration of the gene pool as demonstrated by resistance to DDT. Amer. Natur. 89: 39-46) on the integration of the gene pool. Here resistance of *Drosophila* against DDT can be inherited by the combined alleles of 2 loci, either AA/BB or CC/DD. All the other genotypes did not show any resistance, so the interaction of the 2 loci (epistasis) is responsible for resistance in this case. Crosses between the 2 resistant types would yield non-resistant Aa/Bb/Cc/Dd.

GERHOLD: Dr. Stern, apparently most of your remarks concerning application of quantitative genetic theory pertain to improvement of populations that are in genetic balance. Early in your paper you recommended usefulness of species hybrids. Are not the genetic systems of the first few hybrid generations quite disrupted? Would you comment on quantitative genetic theory to handle such situations?

STERN: I have not covered any quantitative genetic theory here except some applying to resistance. It's quite clear that work with species hybrids has some quite severe limitations on the side of adaptation, growth and like things. However, it might be possible to introduce genes from exotic species having an effect on general (horizontal)

resistance. Perhaps host-parasite equilibrium is possible only if the degree of general resistance is high. Why not try it with species hybrids? Of course this would be experimental, but we're only sure after having performed the experiments.

SCHREINER: As I listen here I wonder whether we aren't making a case for a collection of germ plasm to provide the greatest possible amount of panmixis. In order to develop populations in which we can define this cryptic variability we will have to break up gene associations. Perhaps this is what Wright was referring to when he wrote his paper on preadaptation many years ago. I wonder whether our wheat-breeder friend Dr. Pope would agree that what we need is perhaps a breaking up of some of these gene associations. Are we, perhaps, making a mistake in assuming that we have a very widely heterozygous population in any one stand?

POPE: It's really the same speech over again. Had. Dr. Borlaug commented first there would have been nothing for me to say. He has really done what I was suggesting on a world-wide scale. You can read the plants just like you can read the page of a book. The phenotype of the individual, resistant natural-stand trees tells only part of the story. Bingham's seedling progeny tests tell another part of the story. The progeny, mature-tree testing yet to come will be another part of that story. The only thing I can suggest is that you put your plants together as best you know how, then because we don't know very much about resistance, put them together in many other ways not suggested by what you know now. I would include the wildest possible crossing in logical and illogical ways. The most important findings I have made in wheat have usually been accidents, something I happened to see alongside the plots where I was hard at work. Not much I did on purpose really worked very well. You must put your trees together in a way so that all these "accidents" can happen. These accidental findings will be more meaningful than many of the experiments you plan carefully. But this course of action requires large numbers of parents and larger progenies than now being used.

BINGHAM: In defense of us foresters I would point out that we are necessarily far, far behind crop breeders in gaining--even what the crop-breeder might consider to be background information--on our tree rust resistance systems. First, we began intensive breeding work only about 20 years ago. Second, we face relatively lengthy tree reproductive cycles (with most pines it's 3 years from pollination to 1-year-old seedlings) and even longer resistance testing cycles (3 to 4 years from inoculation to appearance of foliar and early bark resistance reactions). Thus I feel that we first need to gain for tree rusts some of the fundamental knowledge the crop breeder already has and accepts, however unconsciously, as a prelude to his work. I think we must find and be able to recognize specific resistance reactions and vertical resistance genes. This knowledge will help us to do, Dr. Pope, what you may be doing intuitively--recognizing effects of vertical genes and possibly eliminating the ones that you know from experience just don't work here. At present the forester can't do this, even consciously, so I feel we must strive to gain basic information about single resistance genes and their reactions.

POPE: If I may answer, I don't think there is such a thing as a single gene in *complete* control of any character. For instance, in the genetics text books you find a pertinent example having to do with white eye in *Drosophila*, reported as a mutant from red eye and as a single gene effect. This is a beautiful 3:1 example, but the student usually misses a later paragraph pointing out that there is a series of about 40 or 50 known genes that have to function normally before the white versus red eye alternative is possible. A week ago in Pullman, Washington, we had an International Barley Conference. One paper that stuck in my mind was presented by the von Wettsteins, a husband and wife team from Denmark. So far they have deliberately induced some 500 mutants for "waxy" in barley, and they have located 300 of these on 6 of the 7 chromosomes--several of them in allelic series. Every one of these mutants is different. Their objective is 1,000 mutants, just for waxy. Now wax is a little more complex than some simple chemical, but surely it is not the most complicated plant character. If you can induce 500 mutants for waxy and find 300 of them, there are probably 500± variants in all similar characters. Quit thinking about single genes, recognizing them when they go by, and avoid them like a trap.

BINGHAM: I agree, but you recognize the nature of waxy, or white eye to start with.

POPE: The principles behind simple 3:1 ratios is sound; but remember, underneath such obvious relationships is a great big base of genetic variation, and it's mush as far as any recognizable ratios are concerned.

MELAMPSORA PINITORQUA (BRAUN) ROSTR. AND *PERIDERMIUM PINI* (WILLD.) KLEB., INOCULATION PROBLEMS AND TECHNIQUES

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ABSTRACT

The difficulties involved in carrying out inoculation tests with *Melampsora pinitorqua* on pine have been discussed. The handling of dry teliospores does not present much of a problem, but basidia and basidiospores are extremely sensitive to desiccation and higher temperatures.

Concerning *Peridermium pini*, an account is given of a method of inoculating pine shoots with spores suspended in water.

The main biological features of these rust fungi have been known for a long time, but this is not to say that successful methods exist for inoculating them on a large scale in progeny tests.

MELAMPSORA PINITORQUA

Melampsora pinitorqua (Braun) Rostr. twisting rust on pine is but a small part of an extensive *Melampsora* leaf rust complex (Gäumann, 1959). Among the hosts of *Melampsora populina* (Pers.) Lév. group are the genera *Populus*, *Larix* and *Pinus*, and in the *Melampsora salicina* Lév. group are to be found a number of host plants of interest in forestry, including *Salix*, *Abies* and *Larix*. Probably other host plants of practical significance in forestry are also involved. *Pseudotsuga*, for instance, has been mentioned by Longo, Moriondo and Naldini (1967). Studies of American pine species in Europe with regard to *M. pinitorqua* have generally added new species to the list of known hosts (Longo, *et al.*, 1967; Klingström, 1969). A corresponding complex of *Melampsora* species exists in North America. From the point of view of European forestry it is worth noting that in American tests *Pinus silvestris* L. is susceptible to *Melampsora* rusts (Ziller, 1965).

M. pinitorqua occurs in the whole of Europe and in adjacent parts of northern Asia. The fungus infects the annual shoots of pine with basidiospores during the axial extension period. These spores are distributed from telia that have overwintered on the ground on dead aspen leaves. The teliospores germinate in damp weather and, if this coincides with the axial extension of the pines, infection can result. In other words, the occurrence of pine twist rust on pine depends on the fortuitous

coincidence of rainy weather with the brief period of time when the shoots are elongating and receptive to the fungus. The ability of the teliospores to germinate increases with rising spring temperatures, after a chilling requirement is satisfied. Although germination is inhibited very effectively to start with, the inhibition disappears in conjunction with warm weather and rain (Klingström, 1963a). A similar development has been demonstrated under American conditions (Ziller, 1965). The frequency of pine twisting rust changes from year to year under natural conditions and within very wide limits.

In large parts of the southern European range, the fungus is able to overwinter in living aspen twigs. Consequently it is less dependent on host alternation with pine. This has been emphasized in several works (Klebahn, 1938; Regler, 1957; Moriondo, 1956, 1961), but it has not been determined whether the fungus can overwinter in each of the various *Populus* species or hybrids. Overwintering has not been proved in *Populus tremula* L., the most common alternate host in northern Europe, even though Kujala (1950) suggests that overwintering on *P. tremula* occurs. And the observations of Roll-Hansen (1967) seem to make the overwintering on *P. tremula* certain.

MELAMPSORA PINITORQUA - INOCULATION AND INOCULUM

Only a few test reports regarding the inoculation of pine with *M. pinitorqua* are available. Regler (1957) worked with 10 1-year-old and 10 2-year-old pine plants in a greenhouse. Aspen leaves with germinating teliospores were held in close contact with the annual shoots of pine. To some extent Schütt (1964) used the same method, although he also relied on spontaneous infection. Moriondo (1961) tried to isolate individual pine shoots in test tubes together with telia-bearing aspen leaves.

Successful inoculations can be obtained on a small scale, but it is difficult to judge the usefulness of these methods, particularly if a large quantity of pine material is to be treated. Tests have been made with larger numbers of pine plants under nursery conditions (Klingström, 1963a). The host plant material used in the tests was put in shallow beds topped with wire netting. Moist aspen leaves were placed on the netting so that the basidiospores were free to fall on the host material. The leaves were held in position under a cloth which was placed over the wire netting and kept damp for one night. Massive infection of year-old plants was obtained. A similar method has been used in American tests with *Melampsora albertensis* Arth., *Melampsora medusae* Thüm. and *Melampsora occidentalis* Jacks. where individual plants enclosed in plastic bags were exposed to free-falling spores (Ziller, 1965).

Success of inoculation tests with *M. pinitorqua* on pine is affected by the difficulty of working with germinating teliospores and by the extreme sensitivity of basidia and basidiospores. Basidiospores on a moist aspen leaf in a dry atmosphere perish in a minute or so. Further, both teliospores and basidiospores are sensitive to elevated temperatures (Klingström, 1969). Even brief exposure to 25 to 30°C, common in laboratories in the summer, is sufficient to kill the basidiospores. On the other hand, dry aspen leaves can be kept for a long time at low temperatures without any apparent effect on the ability of the teliospores to germinate (Klingström, 1969). The storing of dry inoculum therefore presents no problem, a fact that has been established by other workers (Molnar and Sivak, 1964; Ziller, 1965).

When collecting aspen leaves for inoculum it is necessary to check each year to be sure that the teliospores are germinable. The conditions required for germination, referred to above must be satisfied. If the leaves are soaked in cold water for a few hours and then laid out on a damp surface or in Petri dishes at 15 to 20°C, after a few hours it is possible to detect the formation of basidia with the naked eye. Should the telia either fail to germinate or germinate only after a few days, the aspen leaves were collected too early. However, it is seldom possible to force development of basidiospores on more than a small percentage of the aspen leaves. Also, it is usual for the basidiospores on individual leaves to form simultaneously on only a part of the leaves.

Melampsora species are difficult to identify just from the appearance of teliospores on aspen leaves. This is true particularly where both *Pinus* and *Larix* are common and where *Melampsora larici-tremulae* Kleb. may be as common as *M. pinitorqua*. The situation can be complicated even further by the presence of *Mercurialis*, *Chelidonium* or *Allium*, which can carry aeica of other *Melampsora* spp., all with uredospores and teliospores on species of *Populus*. The situation must be assessed from area to area.

Inoculation experiments on pine plants can be carried out with a degree of certainty, either in the greenhouse or nursery. In nurseries, use must be made of damp weather or a suitable temperature. Night inoculation usually ensures suitable humidity and temperature conditions.

In more extensive field tests, with slightly larger plants, the prospects of controlling infection are reduced. The plants may be brought into contact with aspen leaves carrying teliospores (Klingström, 1963a), but the weather is still the determining factor. If one has a nursery for resistance tests, the pine plants can be watered artificially during axial extension, and then aspen leaves can be introduced or, alternatively, aspen can be cultivated on the test site. While successful test inoculations with *M. pinitorqua* should be possible in theory, as yet no systematic pine resistance tests are being carried out.

The above comments on inoculation of pine with *M. pinitorqua* should be compared with the supplementary information elsewhere in these proceedings which is based on Swedish tests concerning *P. silvestris* and *P. tremula*.[1]

PERDERMIUM PINI

Peridermium pini (Willd) Kleb. is usually described as an autoecious strain of *Cronartium asclepiadeum* (Willd.) Fries. This non-alternating *Peridermium* is extremely common, at least in northwest Europe. Its range within the whole of the enormous distribution area for the host-alternating *C. asclepiadeum*--Europe, North Asia to Korea and Japan--has not yet been fully established. Older works on the taxonomy of *C. asclepiadeum* and the non-alternating *Peridermiume* have been collocated by Bolland (1957), Gäumann (1959), and van der Kamp (1968). And the most recent addition to the scientific naming is *Endocronartium* (Hiratsuka, 1969).

[1] *See paper by A. Klingström, these proceedings.*

Although *P. pini* is regarded as a classic subject in forest pathology, the normal biology of the fungus is imperfectly known. Haack (1914) showed that healthy branches of infected pines could be inoculated with aeciospores if the branches were wounded. Liese (1936) was able to demonstrate that a progeny from a cross between two infected pines was easier to inoculate than the progeny of a cross between two healthy trees. Even these two early works contain suggestions of differences in resistance. However, these tests showed that pines could be inoculated even though they included few pines, made use of large amounts of inoculum, and left the reader uncertain as to how the pines were wounded at the time of inoculation.

Several reports suggest that successful inoculations can be made only on the annual shots of pine - not the needles - and that wounds are necessary (Bolland, 1957; Murray, 1961; Klingström, 1967). On the other hand, van der Kamp (1968) has successfully infected stem wounds and needles. He concluded that infection can take place through stem wounds but that most lesions arise from infection of wounded or unwounded needles. It takes a long time to devise repeatable methods of inoculating on a large scale in the field. Two years elapse between inoculation and the development of aecidia. Current Swedish tests concerned with inoculation methods are still unfinished. However, certain results are available.

PERIDERMIUM PINI - CURRENT SWEDISH EXPERIMENTS ON INOCULATION

Swedish tests have been made under nursery conditions and concern mostly plus tree progenies. Eventually they will entail the inoculation of relatively large numbers of plants, which explains why the tests were made in a nursery. In one test, dry aeciospores were used as inoculum on 20 randomly selected progenies - approximately 4,000 pines between 3 and 5 years of age. Attacks resulted only when the annual shoots were wounded with small punctures of a needle or small wounds with a knife in conjunction with the inoculation. In no instance did a wound to older stem parts or to needles of different ages lead to a successful attack. These initial tests confirmed what was already known. The difficulty of working with dry aeciospores in extensive field tests was quite obvious. This was particularly noticeable where an attempt was made to keep separate spore material from different sources, or to localize the various inoculation sites on the plants. The attack frequency was low in all cases, never exceeding 10 percent of the plant material.

In another exploratory experiment involving 100 plants, an attempt was made to utilize a water suspension of aeciospores dispensed by a medical syringe. Small wounds were made on the surface of the shoot under the drop of spore suspension. In this case inoculation led to the formulation of aeciospores in 10 percent of the inoculations. Brief mention has already been made of this method (Klingström, 1967).

The above line of experimentation formed the starting point of the next series of inoculation trials. Spores were obtained from different geographical areas and kept separate by individual cankers from which collected. The first step always involved inoculating *Paeonia* for the purpose of eliminating the host-alternating *Cronartium*. The next step was to check that the spores were able to germinate on 1% water agar (Klingström,1963b). This ensured that the spores had not been damaged in transit. A check was also made on the viability of the spores in

water suspensions. If dry spores are scattered on water agar they usually germinate after about 5 hours at 20 to 25°C. But spores that were stored in water in a medical syringe for up to 24 hours did not show any sign of germinating in the syringe. If these spores were transferred to an agar surface after 24 hours in the syringe, germination started in the normal way. The mechanism that inhibits germination in water has not been studied. Pine shoots in nurseries were also inoculated with spores that had been stored in the inoculating syringe for various lengths of time. Spores stored for 5 minutes, 1, 3 and 5 hours were used as inoculum to the same pine material simultaneously, and in all cases aecia developed 2 years later on a low percentage of the pines.

Tests were started on pine material consisting of plus tree progenies. The material has been described more thoroughly elsewhere (Klingström, 1967). Only a low percentage of the inoculations resulted in the development of aecia. Had not some individual progenies (and clones) given values of over 10% infection, the tests would have been discontinued. As it was, another series of tests was made using individual host plants that had proved to be susceptible in earlier tests. Unfortunately far too many of these pines died as a result of the first inoculation before the result of the second could be recorded. Another series of tests using susceptible clonal material has been started.

In one test, inoculation was carried out on 159 5-year-old pines selected at random from 53 plus tree progenies. Inoculations were made in three places on each pine, i.e., on three shoots surrounding the terminal leader, near the top of a shoot, in the middle and at the base. The attack frequency was low but did indicate greater success with apical inoculation of shoots.

In another experiment, inoculation was performed on 106 pines from the same progenies. Inoculations were made on shoots of the first whorl by applying a drop of spore solution without making a wound, by applying a drop of spore solution and making one puncture with the injection needle, and by the same procedure plus making 5 and 10 punctures. Aecidia developed only in two cases, both from the treatment involving a single puncture. The only conclusion that can be drawn from this is that the wound as such is necessary, but it can be a very minor one.

At the time of infection in the spring the shoots are still imperfectly lignified and are easily broken off. Damage of this sort is often caused by birds. In an attempt to emulate this some first whorls were broken off and a drop of spore suspension was applied to the fracture. Compared with a puncture made by an injection needle, this is a massive injury. Spore solution placed on 106 such fractures resulted in production of aecia in only three cases.

In another experiment 25 6-year-old pines that were known to be susceptible were used in a second inoculation with the same type of spore suspension used previously (i.e., the spores that formed on the pines were collected and used again to inoculate the same pines). The intention was to discover how long the pines remained susceptible to inoculation. The tests covered the period June 15 to July 27. Pairs of shoots on 1-year-old branches were inoculated, 1 pair each week as long as these shoots were available. The temperature and type of weather were recorded for each inoculation. The result of this test (Table 1) indicates that the pines are susceptible for a considerable time, and that cool weather probably gives lower values for the formation

of aecia. It should be pointed out again that 2 years elapse between inoculation and the development of aecia. Further, it has not been established which climatic factors play a decisive part during this period.

Table 1. Production of *P. pini* aeciospores from 50 inoculations per week performed on 25 6-year-old pines for 7 consecutive weeks

Inoculation date	Temperature at time of inoculation	Weather at time of inoculation	No. of inoculated branches producing aecia 2 yr. later
June 15	28 C	clear, breezy	3
June 22	25 C	partly cloudy rising wind	10
June 29	18 C	overcast, windy	1
July 6	20 C	light showers calm	1
July 13	18 C	partly cloudy breezy	1
July 20	27 C	clear, breezy	1
July 27	21 C	clear, windy	4

Aeciospores can be kept viable for a long time when held at low temperatures. Spores stored at 4°C and -25°C have infected pines after 1 year. Condensation cannot be allowed to form in the test tube in which the spores are stored. Spores collected in damp weather do not store as well as those gathered in dry weather. Their reduced germination, in addition to that caused by the spores' metabolic activity, can also be due to degeneration caused by contaminating Penicillia and similar fungi. Under storage at 20°C, the spores' ability to germinate successively declined during a period of about 4 weeks. At the same time the color of the spores changed from yellow to white.

A generally held opinion about *P. pini* on pine is that the pines show juvenile resistance but are susceptible in the higher age classes. This reflects the common occurrence of the rust on older trees long exposed under natural conditions (Mülder, 1953). Inoculation apparently breaks through whatever barries (real or fancied) there might be.

Even very small plants can be inoculated (Fig. 1), and tests have been successful on year-old plants. A serious obstacle, however, is that many plants die before a definite diagnosis for *Peridermium* can be made. Other fungi, e.g., needle casts, confound the diagnosis. Further, such small plants have only one leader shoot that can be inoculated. Waiting 1 year more makes it possible to utilize both the terminal leader and surrounding shoots. And by then it is unusual for the plants to die before the *Peridermium* attack can be diagnosed with certainty.



Figure 1. Fusiform swelling and pycnial droplets 14 months after inoculation with *Peridermium pini* on a *Pinus silvestris* seedling 3 years old.

Tests have also been made to determine the significance of the concentration of spores in the water-suspension inoculum, but these have not led to conclusive results. It is difficult to make a homogenous suspension of aeciospores in water. Two drops of Tween 80 per liter water make the suspension more stable and do not influence spore germination in laboratory or field tests. In the experiments described above, the number of spores in the inoculum has been about 10,000 per droplet. Tests with mixtures of spores from different collections have also been inconclusive.

SUMMARY

M. pinitorqua has a wide range in the whole of Europe and in adjacent parts of Northern Asia. It is a part of an extensive *Melampsora* leaf rust complex.

Dry aspen leaves with *M. pinitorqua* teliospores can be kept for a long time at low temperatures as inoculum. The germination ability of the teliospores increases during the spring, which makes it necessary always to check the germination ability of inoculum.

Germinating teliospores and basidiospores are very sensitive to dry conditions and higher temperatures. Successful inoculation experiments have been carried out both in greenhouse and nursery, but as yet no systematic pine resistance tests are being carried out.

P. pini is a very common pine-to-pine rust in northwestern Europe; its range in Europe and northern Asia has not yet been fully established.

Most reports on successful inoculations suggest that infection can be made only on the annual shoot and that wounds are necessary.

Current research on an inoculation method with aeciospores suspended in water is described. Even year-old plants can be inoculated as well as older pines. And pines are susceptible during a considerable time in the early summer. The inoculation experiments are influenced by resistance factors, and one obstacle has been to find pine material of a suitable susceptibility.

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FLOOR DISCUSSION

KREBILL: Dr. Klingström, with regard to *Peridermium pini*, you mentioned you have greater success high up on the shoot. I presume this is only in current season growth, or do you also have success throughout the older tissues also.

KLINGSTRÖM: I have tried to inoculate shoots at different points. Near the top of a shoot, in the middle of a shoot, and at the bottom of an annual shoot, and of course, then we come up with blister rust from all inoculations. I obtain perhaps three times more if I make inoculations high up near the top of the shoot.

KREBILL: Have you tried this without puncture wounds and at various stages of development in the new current year shoot?

KLINGSTRÖM: Yes, and I have only had success if I wound the shoots, but on the other hand, the wound can be any type of wound. You can just break the shoot off and apply the spore drops to the broken shoot, or you may just make one little puncture.

KREBILL: Using *Peridermium harknessii*, which is a pine to pine rust, workers in the U.S. and Canada have had excellent results without wounding, but only if they time the inoculation very closely. There is probably about a 2 to 4 week period in which infection will occur. This is somewhere near the time of the emergence of the needles from the sheaths. Consequently, unless you are aware of what tissues are susceptible, you can get very poor results, but when you know something is susceptible, you get very fine results. Some of this ought to be further explored, although I realize that the results by you and van der Camp also indicate this is necessary.

KLINGSTRÖM: I think much of the trouble is found in the pine material which is not susceptible enough. I am sorry to say, we have been working for many years with pine materials which are too resistant; so, now I have crossed quite a lot of susceptible pines and made quite a few grafts. I hope that I can have more success from now on, but it's not funny to wait 24 months for aeciospore formation.

KINLOCH. I believe it's understood that susceptibility to *Peridermium pini* increases with age. Have you tried much older material in your clonal seed orchards or in the wild and have you had more success with or without wounding?

KLINGSTRÖM: The old papers say it's only the older pines that are really susceptible, but with these inoculation methods you can evidently break through whatever barriers there may be. I have made a few inoculations in old pines which are already attacked with *Peridermium pini*, and it's very easy to inoculate them. But it's easy to inoculate very small pines too.

KINLOCH: Would you wound the older pines?

KLINGSTRÖM: Yes.

KINLOCH: That's still necessary even though they are older?

KLINGSTRÖM: Yes, I think so.

KREBILL: Do you think there is some vector relationship involved in infection of *Peridermium pini* in nature?

KLINGSTRÖM: I have seen in nature that the blisters may be consumed by some insect. Now, I just showed this to some entomologists. They shook their heads and could not say what sort of insect it could be. Insects evidently can eat the blister rust and spread away. But I don't know what sort of insect it is.

KREBILL: We also have insects here that do the same thing.

KLINGSTRÖM: I will try to look for that.

BINGHAM: Allan, would you care to comment on van der Kamp's finding reported in his 1968 or 1969 bulletin in respect to the fact that he could account for only 10 percent of the lesions in Scots pine blister rust by wounding of the bark or stem directly? The remainder is a little mysterious regarding exactly what he meant. They seemed to have occurred through wounded or unwounded needles.

KLINGSTRÖM: Yes, it is not too easy to comment on that, but it may be that he has, perhaps, a strain of *Peridermium* which is very infectious. Or, he may have had pines which were very susceptible. All the older literature says that you have to wound the seedlings and you have to wound the shoots and so on. I have made tens of thousands of inoculations, and I have only had success when I wounded the shoot. I shouldn't say that van der Kamp is wrong. He has evidently worked with other materials or he may have wounded the leaves a little bit, because the wound can be very very small. When I apply the drop of spores I have tried to make just one puncture, five punctures, ten punctures. I have always had the greatest success with only one puncture, since it is just a very little wound which is necessary, and the wound can be of any size.

TECHNIQUE FOR INOCULATING PINE SEEDLINGS WITH *CRONARTIUM FUSIFORME*

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ABSTRACT

An apparatus has been devised for inoculating pines with uniform numbers of *Cronartium fusiforme* basidiospores. Inoculum densities are regulated by adjusting the time that seedlings are exposed to an airstream which carries the spores and by regulating the rate of airflow. The method has produced 99 percent infection of pines.

An apparatus for applying uniform amounts of basidiospores to test plants has been developed at our laboratories in Gulfport. It is currently being used to inoculate pine seedlings with *Cronartium fusiforme* Hedgc. & Hunt ex Cumm. It has been described before (Snow, 1968), but several modifications have improved its efficiency.

The device consists of two plexiglass boxes connected by a brass tube (Fig. 1). After telia on oak leaves have been induced to sporulate in the large box, individual pine seedlings are placed in the small box with the tuft of juvenile needles against the connecting tube. A vacuum line to the small box creates a flow of moist air that carries falling spores to the pine seedlings. The air entering the system is moistened by forcing it through gas-dispersion tubes in two bottles of water. A bleeder valve in the second bottle improves uniformity of airflow.

Before plants are inoculated, a glass cover slip is exposed to the airstream (2 mm from the connecting tube in the small box) for a measured time and at a given rate of airflow. The cover slip is examined to determine the number of spores per square millimeter. Spore density is then regulated by adjusting time of seedling exposure and rate of airflow. Adjustment is accomplished with a timer for the vacuum pump, and an airflow regulating valve. Calibration runs and readjustments are made after 8 to 10 plants are inoculated in succession. Spore densities of 30 to 60 spores per square mm have been maintained in several experiments (see Kais and Snow, a second paper in these proceedings) with exposures of 5 to 60 seconds per seedling at airflow rates of 3 to 10 liters per minute. During inoculation the plexiglass boxes are held in a cabinet that is maintained at 20±0.1 C and is continuously moistened with a humidifier. Seedlings are also atomized with distilled water before and after inoculation. The inoculated seedlings are transferred to moist chambers in the cabinet and are incubated in these chambers for 24 to 48 hours.

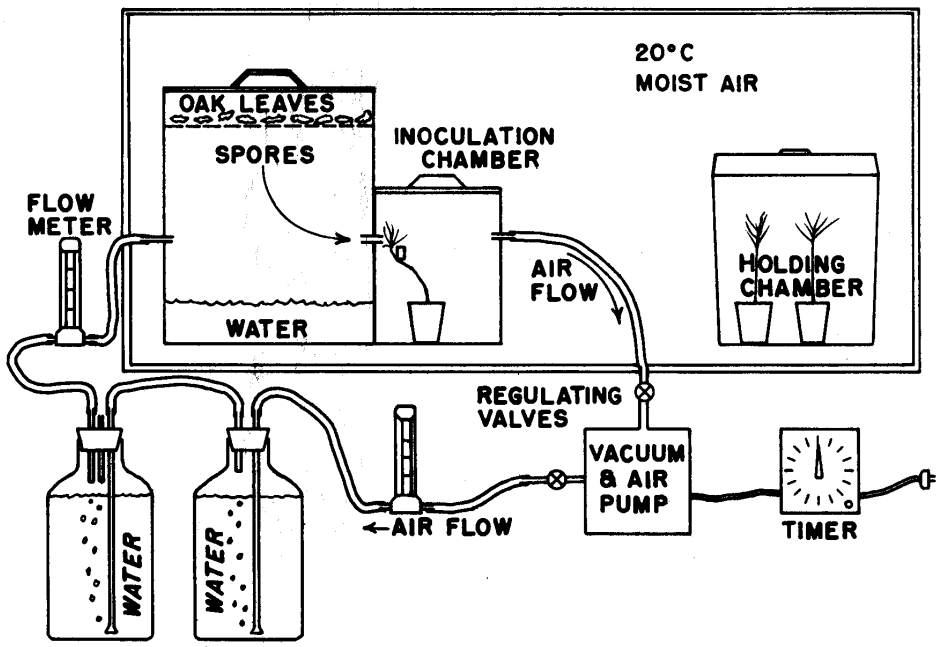


Figure 1. Apparatus for inoculating pine seedlings. Basidiospores of *Cronartium fusiforme* released from telia on oak leaves in the large compartment are carried by a stream of moist air through the connecting tube to the tree in the small compartment.

We have inoculated up to 200 seedlings with one collection of telia. Oak leaves usually begin shedding sufficient basidiospores within 5 to 6 hours after being placed in the system. Inoculation of 200 seedlings--including time for repeated calibration runs--requires 3 to 4 hours. The uniformity of the technique allows us to use fewer plants in an experiment than would be required with a less efficient method. In a recent study, 536 pine seedlings were inoculated and all but 3 developed symptoms of fusiform rust.

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Snow, G. A. 1968. Time required for infection of pine by *Cronartium fusiforme* and effect of field and laboratory exposure after inoculation. Phytopathology 58: 1547-1550.

FLOOR DISCUSSION

Panel leader Patton withheld discussion on this and three other papers covering *C. fusiforme* inoculation problems and techniques until after the last (R. A. Schmidt) of the papers. Discussion of all four papers will be found there.

AN INOCULATION SYSTEM FOR *CRONARTIUM FUSIFORME*

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ABSTRACT

Standardized techniques for inoculations with *Cronartium fusiforme* are lacking. A technique is outlined permitting inoculation of up to 1,000 pine seedlings at a uniform, reproducible, and controllable basidiospore density. Basidiospores of *C. fusiforme*, naturally abjected from telial columns on oak leaves, are carried into an inoculation chamber in a stream of air maintained at near spore temperature and moisture optima. Densities of 100,000 spores/cu ft have been attained. Relation of density to infection is being studied to determine density optima for future work utilizing the technique.

Research studies on fusiform rust of southern pines are frequently handicapped because the standard inoculation procedure of suspending telia-bearing oak leaves over young pine seedlings gives highly variable results. This is due primarily to fluctuations in inoculum density. The inoculation technique outlined here was designed to overcome this limitation. It allows for the inoculation of large groups of pine seedlings with a uniform, reproducible, and closely controlled sporidia density.

The basic principle utilized is that *Cronartium fusiforme* Hedgc. and Hunt ex Cumm., as well as other rust fungi, naturally abject their basidiospores. By passing temperature-controlled, water-saturated air beneath the telial columns of *C. fusiforme*, the sporidia are swept into an inoculation chamber and uniformly deposited on pine seedlings in much the same manner as in nature. Recently Snow (1968b) utilized this principle and reported on an apparatus that inoculates tufts of primary needles of individual pine seedlings with sporidia of *C. fusiforme*.

Temperature, relative humidity, and rate of airflow are the most important environmental factors to consider. The design specifications, therefore, called for construction of a system that controlled these factors close to the environmental optimum for *C. fusiforme*.

The inoculation system is shown in Figure 1. Compressed air is bubbled through distilled water in 4-liter Erlenmeyer flasks held at 34 C in a constant temperature water bath to provide maximum humidity. The airflow meter for each of the three lines (0.95 cm ID Tygon tubing) to these humidification flasks is normally adjusted to 70 liters per minute (LPM). Another airstream, similarily adjusted, is bubbled through distilled water in a 4-liter Erlenmeyer flask held in a cold water bath (5 to 10 C).

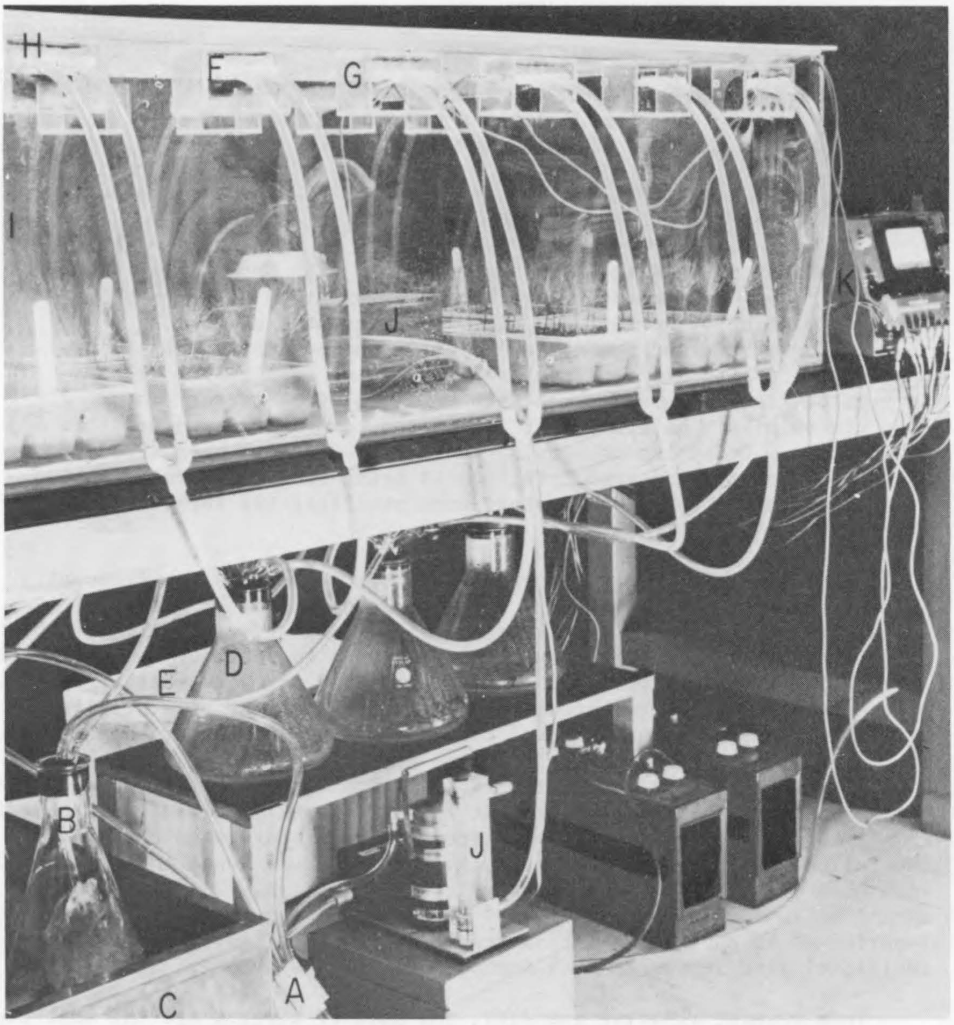


Figure 1. Apparatus for inoculating pine seedlings. Basidiospores of *Cronartium fusiforme* abjected from telia on oak leaves (H) suspended over the internal ports (G) are carried by a stream of moist air into the inoculation chamber (I) containing the pine seedlings. Other components of the system are the air-streams (A) to the humidification flasks (B) held in a constant temperature (34 C) water bath (C), air-mixing flasks (D), cold water bath (5-10 C) (E), modified Nalgene "T's" (F), Kramer-Collins spore sampler (J), and scanning tele-thermometer (K).

The humidified air is then mixed with the cool air in three 2.8-liter Fernbach flasks which also serve to accumulate excess moisture. Temperature control is accomplished by balancing airflow from the humidification and the cooling flasks without altering the total airflow (280 LPM) through the system. The leads from the humidification flasks and those from the Fernbach flasks to the inoculation chamber are connected so that the chamber is not directly influenced by any one airstream. A scanning telethermometer, chart recorder, and 11 temperature probes located at various points in the inoculation chamber are used to determine that the temperature is held at 21±0.5 C throughout the chamber when set up in an air-conditioned laboratory. Further temperature control is easily accomplished by placing the system in a controlled environment chamber.

The temperature-controlled, saturated air from the Fernbach flasks is passed into the upper portion of the inoculation chamber through 0.63 cm Nalgene "T" connectors. A row of six, small (1 mm), evenly placed holes was made with a hot needle on the facial surface of each "T" and both ends were plugged with silicone rubber.

Twelve internal ports (10 cm long by 5 cm wide by 6.25 cm high) made of "Plexiglas", six equally spaced on each longitudinal side of the inoculation chamber, contain telia-bearing leaves. Each port contains two modified Nalgene T's. The "Plexiglas" port covers are large enough (5 cm x 10 cm) to hold 24 0.85 sq cm discs of telia-bearing leaves. The leaf discs are preconditioned for 5 or 6 hours at 20 C in a saturated atmosphere and then attached with 2% (w/v) water agar to the port covers so that the telia are suspended directly over the incoming airstream.

The inoculation chamber is made of 0.63 cm "Plexiglas"--1.27 m long by 63.5 cm wide by 30.6 cm high. The chamber is large enough to hold 12 plastic plant-flats (18 cm x 23 cm x 5 cm) containing 6- to 8-week-old pine seedlings. Each flat can hold from 20 to 80 seedlings, depending on whether or not the seedlings are to be transplanted after inoculation. With this system it is possible simultaneously to expose from 240 to 960 pine seedlings to the same sporidia density. After inoculation, the seedlings are immediately transferred to an incubation chamber with a saturated atmosphere at 20 C for 18 to 24 hours.

A Kramer-Collins spore sampler (Kramer and Pady, 1966) placed in the center of the chamber determines the number of sporidia per hr/ft^3 of air sampled. Two-week-old telia of *C. fusiforme*, approximately 700 telia per port, and an inoculation period of 8 hours provide a total inoculum density of approximately 20,000 sporidia/ft^3. By adjusting the number of telia per port, densities as high as 50,000 to 100,000 sporidia/ft^3 can be attained. These densities are well in excess of those recorded under natural conditions (Snow, 1968a,c).

Although evaluation of this system is still in progress, completed tests indicate that inoculum density can be closely controlled by controlling the telial density on oak leaves, telial age, and number of telia per port. The relation of inoculum density to infection is now being studied to determine the optimum density for future studies utilizing this system.

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Snow, G. A. 1968b. Time required for infection of pine by *Cronartium fusiforme* and effect of field and laboratory exposure after inoculation. Phytopathology 58: 1547-1550.

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FLOOR DISCUSSION

Panel leader Patton withheld discussion on this and 3 other papers covering *C. fusiforme* inoculation problems and techniques until after the last (R. A. Schmidt) of the group of 4 papers. Floor discussion of all four papers will be found after Dr. Schmidt's paper.

TESTING FOR FUSIFORM RUST RESISTANCE IN SLASH PINE

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ABSTRACT

Similar results were obtained in artificial and field tests for resistance to the fusiform rust fungus (*Cronartium fusiforme*) in open-pollinated progenies of six slash pines (*Pinus elliottii*). In two artificial inoculation tests, resistance was reliably identified in 9 months. At least 4 years were required to distinguish resistant from susceptible lines in two field tests. The proportion of plants infected was a better measure of field performance than numbers of stem infections or total numbers of infections. One selection performed poorly under artificial conditions but better than average in the field. Its form of resistance apparently differed from that of selections that performed well in both tests.

INTRODUCTION

Since fusiform rust, caused by *Cronartium fusiforme* Hedgc. and Hunt ex Cumm., is the most serious disease of slash pine (*Pinus elliottii* Engelm.), identifying resistance to it is vital to the success of tree improvement programs for slash pine. Tests to locate resistant selections can be performed by exposing progenies to uniform, abundant supplies of inoculum under artificial conditions or to natural levels of inoculum under field conditions. Jewell (1960) devised an artificial inoculation technique in which telia-bearing leaves are suspended over pine seedlings in the cotyledon stage under controlled conditions of temperature and moisture. Subsequently, the capacity and efficiency of this method have been increased (Jewell and Mallett, 1964, 1967). This and related approaches (Arnold and Goddard, 1966; Davis and Goggans, 1968) may be too severe a test, however, since selections having slight but useful resistance may be eliminated. Resistance to some diseases varies with age (Patton, 1961), so tests on juvenile material could be misleading. Furthermore, testing at only one age with local inoculum could result in selection for specialized rather than generalized resistance (Smith, 1968).

While some of the potential shortcomings of artificial inoculation are not experienced in field trials, the latter are costly and time consuming, and they too may be unreliable. In some cases, infection rates under field conditions have fluctuated widely from location to location and year to year (Henry and Jewell, 1963; Kinloch and Kelman, 1965; LaFarge and Kraus, 1967).

This paper describes infection rates under artificial conditions and compares them to those observed in field plantings at a number of locations and after several years of exposure.

METHODS AND MATERIALS

Six slash pines were selected in Harrison County, Mississippi, for use in artificial and field tests (Jewell and Mallett, 1967). Three were rust-free (8-7, 11-6, and 18-27) and three were infected (18-40, 18-41, and 18-62). The natural stands involved were about 75 percent infected. Open-pollinated seeds were collected for several years from each of the six selections.

Dr. F. F. Jewell[1] artificially inoculated open- pollinated progenies of the six trees in identical randomized block designs in 1963 and 1964. Each family was represented by two row plots of 18 trees in each of five blocks. Proportions of plants infected per row were determined 9 months after inoculation. Results of one of the individual experiments were reported previously (Jewell and Mallett, 1964). For presentation here, the original data were reanalyzed as separate tests and as a single experiment combining both years. The proportion of plants infected was transformed to degrees of angle = arcsin $\sqrt{\text{percent}}$ and subjected to analysis of variance for the randomized block design with intra-block replication (Steel and Torrie, 1960). Family means were compared by multiple range tests at the 0.01 level.

Field tests of open-pollinated progenies were established by Jewell in 1963 at Gulfport, Mississippi, and in 1964 on Crown Zellerbach Corporation land near Bogalusa, Louisiana. The Gulfport planting contains progenies from all six selections in a randomized block design. Each family is represented by two row plots of 15 trees in each of seven blocks. The Bogalusa planting consists of five blocks each containing two row plots of 15 trees; five families (all but family 18-41) are represented.

Rust infection was measured annually in terms of three indices: number of stem infections per plant, total number of infections per plant, and proportion of plants infected per row plot. The proportion infected in the latest year was also analyzed after plants previously infected but currently rust-free had been deducted. In each case, proportions were transformed to degrees of angle = arcsin $\sqrt{\text{percent}}$. Plot means for the four variables were subjected to analysis of variance for the randomized block design with intra-block replication. A combined analysis of both field tests was not attempted as the effect would have been confounded with different periods of exposure. Family means were compared by multiple range tests at the 0.01 level. In addition, simple phenotypic correlations were calculated to determine which index best measured infection.

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RESULTS

ARTIFICIAL INOCULATION

Variation among families was significant in both 1963 and 1964. In both tests, the proportion of diseased offspring from one rust-free and the three infected selections was greater than from the two remaining rust-free selections (Fig. 1). The combined analysis of variance confirmed the significance of the family variance, but both the year x family interaction and differences between years were non-significant.

FIELD INFECTION

Stem infections appeared within 1 year of planting at both locations. Since then, the number per plant has increased steadily and significant differences among families were noted as early as 2 years after planting. Although few changes in family ranking have occurred since, considerable variability was encountered within families. For example, the coefficient of variation at Gulfport ranged from 108% during the second year to 65% in the fifth year. By then, progenies of 18-40 and 18-62 had more stem infections than those of any of the other four selections (Table 1). In addition, progeny of 8-7 at Gulfport had fewer stem infections. Simple correlations between numbers of stem infections and other infection indices were significant at the 0.01 level.

Table 1. Mean numbers of fusiform rust infections per plant among open-pollinated slash pine progenies in the field

Location	Family	Number of infections per plant	
		Stem	Total
Gulfport, year 5	18-62	0.65[a]	1.71
	18-40	.60	1.72
	18-27	.36	.87
	11- 6	.32	.62
	18-41	.31	.78
	8- 7	.02	.04
Bogalusa, year 4	18-62	.42	1.46
	18-40	.40	1.90
	18-27	.20	1.19
	11- 6	.14	.52
	8- 7	.04	.05

[a] *Values connected by the same vertical line do not differ significantly at the 0.01 level according to Duncan's test.*

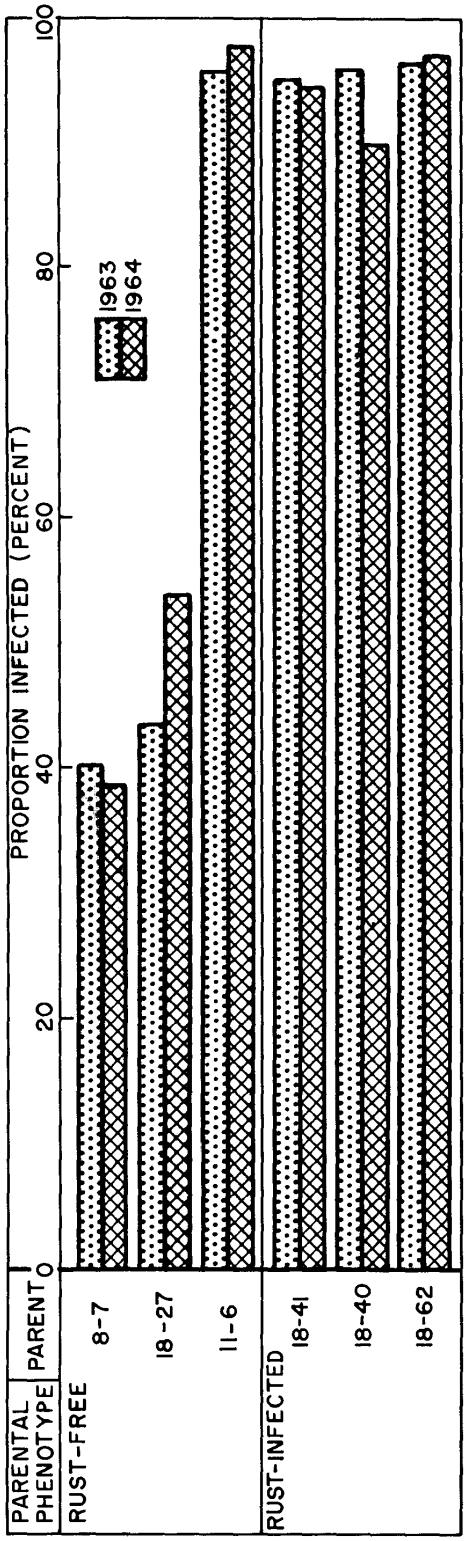


Figure 1. Fusiform rust infection in 6 open-pollinated slash pine progenies 9 months after artificial inoculation, separate tests of the same progenies in 1963 and 1964.

Increases in the total number of infections per plant occurred each year and were consistently larger for progenies of rust-infected selections. However, the frequency of new infections differed greatly between years and also between locations in any one year. In addition, considerable variability existed within families. Coefficients of variation decreased with years of exposure, but were never less than 41%. However, differences among families have been significant since the second year and family ranking has changed only slightly since the third year. At Gulfport after 5 years of exposure, progenies of 18-40 and 18-62 had more infections than those of any of the other four selections (Table 1). Progenies of 18-41, 18-27, and 11-6 had fewer infections, but more than those of 8-7. A similar pattern emerged at Bogalusa after 4 years (Table 1). Progenies of 8-7 and 11-6 had fewer infections than any others. The simple correlation between the total number of infections and the proportion infected was significant at the 0.01 level.

Annual increases in numbers of newly infected plants varied between years and locations (Fig. 2). However, family rankings have been similar at both locations since the third year. Initially, variation within families was large, but coefficients of variation have been less than 30% since the third year. Consequently, differences which were evident among families within 2 years of planting have become more definite. Regardless of location, fewer progeny of 8-7 were infected than of any other selection (Fig. 2). On the other hand, progenies of 18-62 and 18-40 were by far the most frequently infected. Progenies of one rust-infected (18-41) and two rust-free selections (18-27 and 11-6), exhibiting intermediate levels of infection, differed significantly from both the least and most heavily infected families. When plants that were previously infected but had recovered were deducted from totals at the last examination, results were essentially the same (Fig. 2).

DISCUSSIONS AND CONCLUSIONS

Resistant families were apparent within 3 years of planting regardless of location or index of infection. However, variability within families was such that at least 4 or 5 years of field exposure were required for accurate evaluation. The agreement of family rankings at the two field locations indicates that the genetic control of resistance is stable and little affected by interaction with these two environments. Kinloch (1968) reached a similar conclusion for loblolly pine (*P. taeda* L.) planted on a larger number of sites. The three indices of infection gave the six families similar ratings and were significantly correlated. However, the proportion infected seemed the most reliable in view of the large error terms encountered in analyses based on the other indices. Results from the proportion of plants infected paralleled those obtained after adjustment for plants previously infected but not showing infection at the last measurement. This agreement demonstrates that a single scoring 4 or 5 years after planting can provide a realistic estimate of field performance, at least in well-replicated test plantings.

Combined analysis of the two artificial inoculation tests demonstrated that the technique yields consistent results. Progenies of 8-7 and 18-27 resisted artificial inoculation and performed better than average in the field (Fig. 3). While not best in the field, progeny of 18-27 were significantly more resistant than the worst families. Since both these selections demonstrated heritable resistance in both types of test, it appears that they can be used safely in breeding programs as

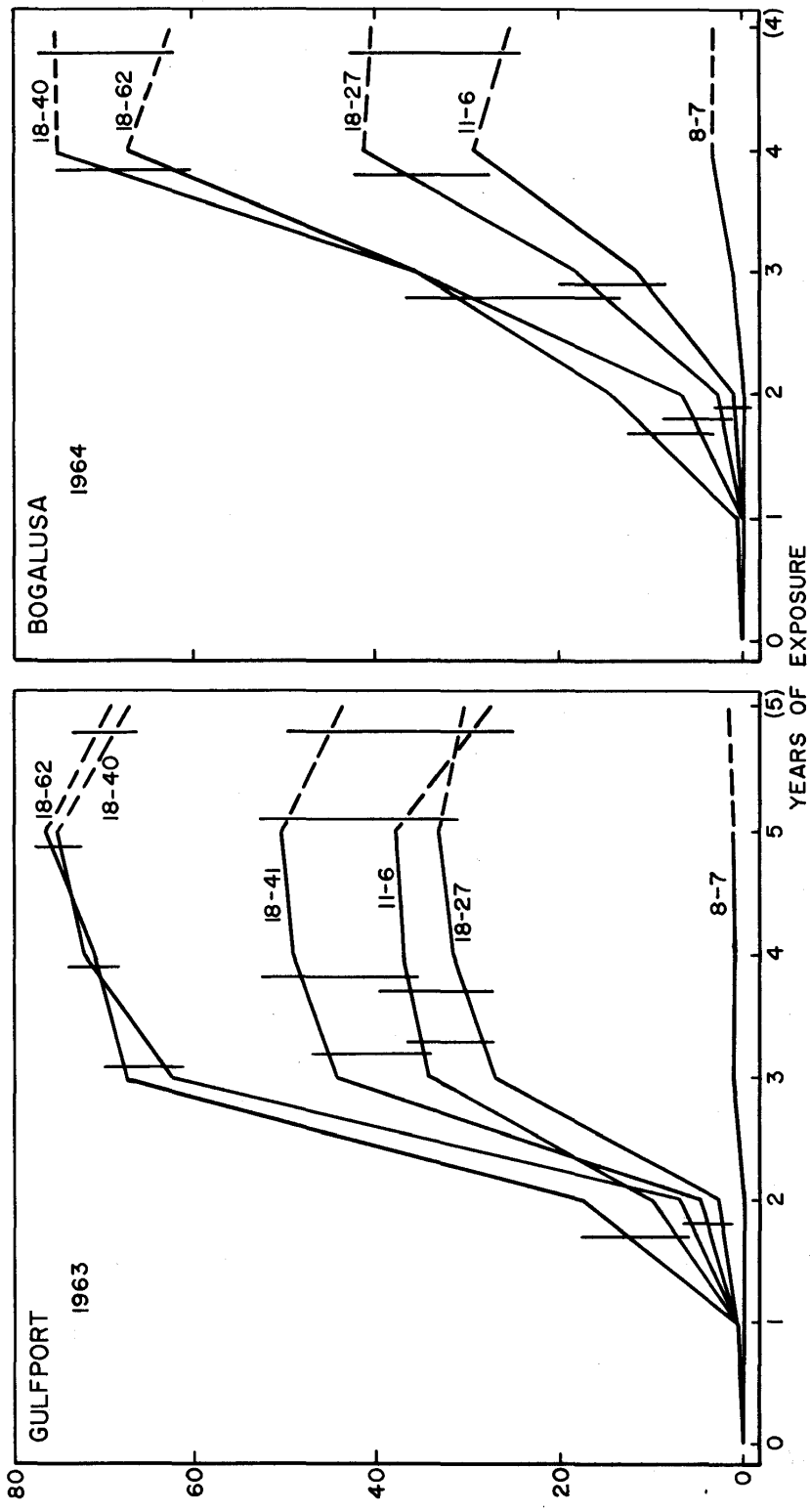


Figure 2. Fusiform rust infection in 5 or 6 of the same open-pollinated slash pine progenies as in Figure 1, 4 to 5 years after natural inoculation in 2 field tests. Values connected by vertical lines do not differ significantly at the 1 percent level, according to Duncan's multiple range test. Values above final years (in parentheses) are percentages after removal of infected plants that recovered.

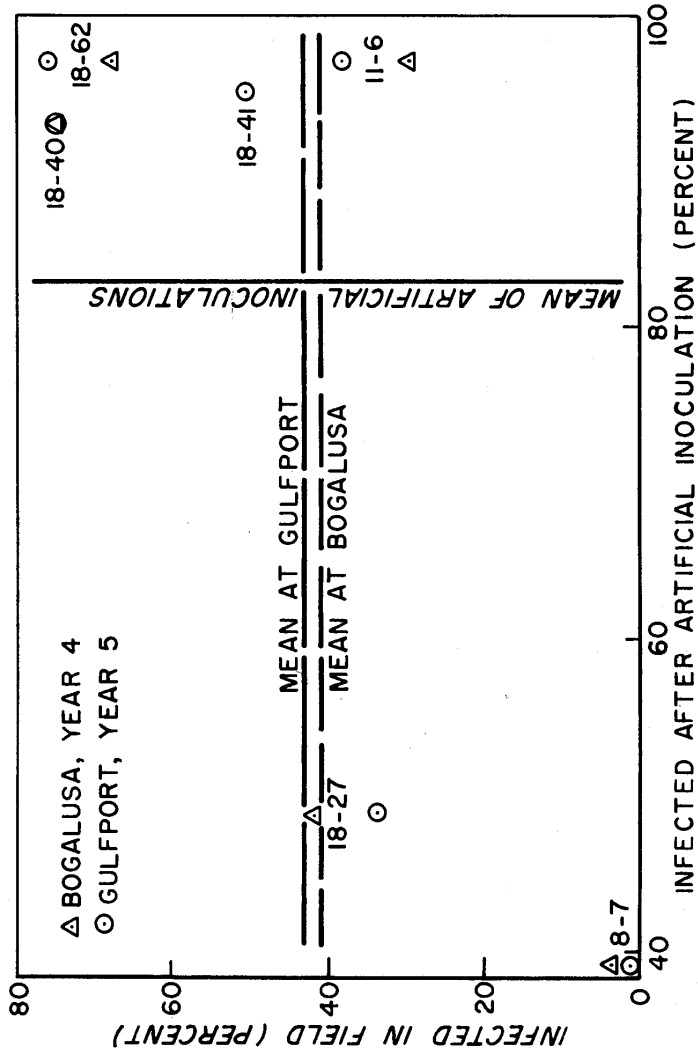


Figure 3. Comparison of fusiform rust infection following artificial and natural inoculation of the same open-pollinated slash pine progenies.

suggested by Jewell and Mallett (1967). This conclusion seems especially sound as these were open-pollinated progeny from a rust-free selection in a stand that was 75% infected. Even better field performance can be expected from crossing individuals thus identified. For example, progeny from the cross between 8-7 and 18-27 or its reciprocal averaged only 10% infection in a series of artificial inoculations (Jewell and Mallett, 1967). Consequently, selection and breeding on the basis of artificial inoculation results should yield rapid improvement.

Judgments based on artificial inoculation results err only on the safe side. Of the progenies resistant to artificial inoculation, none were found susceptible in the field (Fig. 3) even after several years of exposure at two locations. While some potentially useful selections may be overlooked, susceptible ones will not go undetected.

According to results of the artificial inoculation tests (Fig. 1), the infected selections, 18-62, 18-40, and 18-41, are undesirable for inclusion in breeding programs. The presence of 18-62 and 18-40 in the upper right quadrant of Fig. 3 supports this conclusion and further demonstrates the close agreement between artificial and field testing. While 18-41 seems undesirable at first glance, its intermediate field performance (Fig. 2) makes outright rejection questionable. Assuming that resistance is controlled by additive genes (Kinloch, 1968) or at least not by a single dominant gene (Jewell and Mallett, 1967), this intermediacy suggests that 18-41 possesses some genes for resistance. That is, it has a larger complement than 18-62 or 18-40, but smaller than 8-7. Data from previous artificial inoculations (Jewell and Mallett, 1967) support this inference. Progeny from crosses of 8-7 to 18-40 and 18-62 were 42 and 44% infected respectively. Crossing 8-7 with 18-41, however, produced progeny which were only 23 percent infected.

Relying on the artificial testing of open-pollinated progenies would have eliminated 18-41. Thus, such tests may be too severe, but they identify the most resistant selections several years before field tests would. The accumulated data suggest a means of circumventing this weakness. For example, partially resistant and potentially useful selections such as 18-41 can be identified by screening control-pollinated progenies or at least progenies of crosses between candidates and specific tester parents like 8-7.

The rust-free selection, 11-6, performed better in the field than might have been expected on the basis of artificial inoculation alone (Fig. 3). Its performance in other Gulfport plantings has also exceeded expectation. This deviation from agreement infers that 11-6, like 18-41, possesses fewer genes for resistance than 8-7 or else has a different form of resistance. Available evidence favors the latter premise. First, 11-6 performed quite differently in the two types of test. Second, artificial inoculation of progeny from crosses of 11-6 to 8-7 and 18-27 resulted in 53 and 56% infection respectively (Jewell and Mallett, 1967). Progeny from its cross to 18-62 were 95% infected. Thus, 11-6 did not combine as well with resistant selections as 18-41 and was highly susceptible in combination with a susceptible selection.

The field resistance of 11-6 may be dependent upon age or interaction with the environment for its expression. An increase in resistance to blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) with age was observed by Patton (1961). On the other hand, the progeny of 11-6 tended to

the slowest growing of those tested. Hence, its resistance may be an indirect result of mediocre growth. Low vigor and resistance are often related in cases of obligate parasitism (Heimburger, 1962; Illy, 1966). Whatever the underlying causes, the departure of 11-6 from agreement demonstrates that joint artificial and field tests can identify selections having different forms of resistance.

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FLOOR DISCUSSION

Due to late submission this paper was not presented by Dr. Dinus at the Study Institute except in summary form, from the floor. Floor discussion was withheld until after the following, related paper by Dr. R. A. Schmidt.

A LITERATURE REVIEW OF INOCULATION TECHNIQUES USED IN STUDIES OF FUSIFORM RUST

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ABSTRACT

Inoculation techniques used in studies of fusiform rust (*Cronartium fusiforme*) are summarized, covering both mass inoculations and individual tree inoculations. Purposes, results, advantages, and disadvantages of each technique are listed. Infection processes and conditioning factors which affect successful inoculations are discussed, as are inherent advantages and disadvantages of natural and artificial inoculations. A scheme utilizing both types for screening pine for fusiform rust resistance is outlined. Some consideration is given to the evaluation of rust resistance and also to areas in need of further investigation.

INTRODUCTION

Although the inoculation of pine with sporidia of *Cronartium fusiforme* Hedgc. and Hunt ex Cumm. is only one of the many interactions in the fusiform rust disease of southern pine, it is, perhaps, the most important to researchers interested in the identification of rust resistant trees. In order to identify resistant plants, one must create an epidemic and this necessitates a successful inoculation technique. It does not suffice to use only a technique which consistently produces diseased plants. It is necessary to perfect a technique which approximates inoculation under natural conditions. A technique which negates useful field resistance in the test population may have limited application. For example, a method which injects sporidia into the stem bypasses all foliar resistance mechanisms, as well as mechanisms for resistance to penetration of the stem. However, these unnatural inoculation techniques may have utility in studies of the mode of resistance or other disease phenomena.

Inoculation is most often defined as the arrival of the inoculum at the infection court. In the case of airborne fungus spores, e.g., sporidia of *C. fusiforme*, inoculation is in effect the process of deposition. Although subsequent germination and penetration are implied in successful inoculations, they are separate processes. Likewise, colonization and symptom development are separate entities; conventionally the latter signals the end of the incubation period. For the most part, the success of inoculation techniques in fusiform rust resistance research is judged by the presence of foliar lesions or stem galls. This involves (1) germination of telia (production of sporidia), (2) deposition of sporidia onto

susceptible tissue, (3) germination of sporidia, (4) penetration of the suscept by the germinating sporidia, and (5) subsequent colonization. Therefore, many factors other than inoculation *per se* are involved and the term "successful inoculation", as used herein, implies the development of at least foliar symptoms. Table 1 lists some of the requirements for successful inoculation. Little is known about factors affecting deposition, penetration, or post penetration phenomena.

INOCULATION TECHNIQUES

INOCULATION OF PINE

The techniques dealing with the inoculation of pine are arbitrarily divided into those involving relatively large numbers of trees (mass inoculations) and those made on one tree (individual tree inoculations). Mass inoculations are used extensively in screening trials for the identification of rust resistant pines while individual tree inoculation techniques are useful for studies of fungus taxonomy, the host range of the pathogen, the mode of resistance, etc. Both techniques are used in investigations of the epidemiology of fusiform rust. A summary of each technique, including literature citations, purposes, results, advantages and disadvantages, is provided in Table 2. The number and name of the technique in the table corresponds with that in the text where only a brief resumé is given. Techniques presently being developed are included as unpublished reports.

A. Mass Inoculations

Mass inoculations can accommodate relatively large numbers of seedlings and involve the deposition of sporidia onto the surface of test plants. Mass inoculations differ from one another with respect to the control of (1) inoculum density (the number of sporidia deposited per unit area of the test plant), (2) the timing of inoculation (when spores are deposited in relation to when pine tissues are susceptible), (3) the age of suscept tissue, (4) the temperature and/or relative humidity at the infection court, and (5) the geographic interaction. Geographic interaction is used here to identify that interaction among suscept, pathogen, and environment that can condition differential susceptibility of a given genotype planted in different geographic locations. It is of prime importance to consider geographic interaction when climate or racial variation of the pathogen differs among sites.

1. Natural inoculations.--Natural inoculations, i.e., those in which trees are exposed to inoculum under natural field conditions, are of two kinds. These are (1) experimental plantings that are established to evaluate factors such as rust resistance, survival, or growth rate, and (2) natural stands and plantations established for production of wood. The latter, although not established to provide data, yield useful information on the incidence of fusiform rust in relation to cultivation, fertilization, year of planting, age of tree, stand density, etc.

Problems associated with natural inoculations center around the difficulty of controlling inoculum density, time of inoculation, and temperature and relative humidity at the infection court. The resulting variability in the intensity of disease from year to year and among sites makes the identification of resistant genotypes a slow and sometimes

Table 1. Important factors in the inoculation of pine with sporidia of *C. fusiforme*

Infection process and important factors	Conditions	Reference
GERMINATION OF TELIA		
(a) age of telial column at maximum spore production	∿ 2 weeks old	Powers and Roncadori, 1966
(b) optimum temperature	∿ 21°C	Siggers, 1947
(c) atmospheric moisture	≥ 97% R. H.	Snow and Froelich, 1968
(d) time required for: (1) initiation of sporidial production at optimum conditions	4-12 hrs.	Siggers, 1947; Kais, 1963; Powers and Roncadori, 1966; Koenigs, 1968
(2) maximum sporidial production at optimum conditions	6-16 hrs. depending on age of telial column	Powers and Roncadori, 1966
(3) initiation of sporidial production at sub-optimum temperatures	∿ 1 1/2-14 hrs. depending on temperature and preconditioning treatments	Snow, 1968a
(4) maximum sporidial production at sub-optimum temperatures	4-16 hrs. depending on temperature and preconditioning treatments	Snow, 1968a
GERMINATION OF SPORIDIA		
(a) direct: (1) optimum temperature	22°C	Siggers, 1947
(2) time required at optimum conditions	∿ 2 hrs.	Siggers, 1947
(b) indirect: temperature	occurs at 20-22°C	Kais, 1963; Miller and Roncadori, 1966
PENETRATION BY SPORIDIA		
time subsequent to deposition required for successful colonization as judged by symptom development	a minimum of 4 hrs; % infection increased with time of "incubation period"; depending upon post-deposition treatment	Snow, 1968b

uncertain process. Although the time, expense, and space involved in the establishment of meaningful field tests is considerable, their ability to test geographic interactions is an extremely important advantage.

2. Rust nursery.--This technique is essentially one of natural inoculation. Pines to be inoculated are planted between rows of susceptible oaks which are inoculated with aeciospores of the fungus. Irrigation maintains high moisture levels. Although the nursery cited in Table 2 encompasses only one site location and has had erratic inoculation success, the technique has the advantage of closely approximating a natural situation under conditions which enhance the chance of successful inoculation.

3. Tent chambers over nursery beds, etc.--This method, which consists of enclosing in a cheesecloth tent a nursery bed containing seedlings, is used with good success. High moisture conditions within the tent are maintained by a water mist system and abundant inoculum is provided by branches of telia-bearing oak leaves. Inoculum density is difficult to control and some aspects of geographic interaction are normally precluded.

4. Screening shed.--This technique uses a large frame building with screen sides and removable canvas covering. High moisture levels are maintained by spraying water onto the canvas sides. Evaporation from the wet canvas aids in maintaining favorable temperatures within. Seedlings in greenhouse flats are placed on multi-shelved racks within the shed. Abundant inoculum is provided by suspending branches of telia-laden oak leaves above the shelves of flats containing the seedlings, or by placing individual leaves on a wire shelf above the seedlings. This technique can be used with good success to inoculate large numbers (10-15 thousand per test) of seedlings for progeny tests. However, it requires considerable labor to handle the seedlings and provides little opportunity for control of inoculum density or geographic interaction.

5. Inoculation chambers.--In contrast to the large chambers just discussed, several smaller inoculation chambers of various sizes and construction are used to facilitate inoculation of pine. Although the number of seedlings inoculated is relatively small (200-1000), several have been used to screen progeny for disease resistance. Others are designed to study the effects of environment or inoculum density on disease development. These small chambers offer little prospect of testing geographic interaction in relation to disease resistance. Their chief advantages relate to their ability to control one or more of the many variables involved in the inoculation process and, as such, are extremely useful. One such chamber is described in this proceedings (see Dwinell).

B. Individual Tree Inoculations

Inoculation techniques for individual tree are of widely divergent types and, with the exception of techniques No. 6 and 7, Table 2, bear little resemblance to mass inoculations. Individual tree inoculations are not efficient for rust resistance screening programs but are advantageous in other investigations of disease resistance or epidemiology.

6. Telia suspended above individual seedlings.--This technique does not differ appreciably from some mass inoculation methods already mentioned. Usually, oak leaves bearing mature telia are placed directly on each seedling to be inoculated. This method has been used in conjunction

with tent chambers constructed over nursery beds or in greenhouses. Although it is time consuming for large studies and difficult to control inoculum density, the method can be used to good advantage to provide abundant inoculum for each seedling and, thereby, increase the chance for successful inoculation.

7. Inoculation chamber.--In this proceedings, a chamber for inoculation of individual seedlings is described (see Snow and Kais). This two-compartment plexiglass box is designed to control inoculum density, temperature, and relative humidity for epidemiological studies. The disadvantages of this chamber arise from its single plant capacity. However, for many studies, the advantages which accrue from the control of important variables far outweigh the disadvantages.

8. Water suspensions of sporidia.--Sporidia cast from germinated telial columns can be suspended in water and sprayed onto susceptible pine foliage. This technique, which is not wholly unnatural, usually did not result in the successful establishment of the fungus in pine tissues. In addition to separating telial germination from sporidial germination, this technique provides a means of quantifying inoculum density and, therefore, is a candidate for further study.

9. Direct placement of precast sporidia onto pine tissue. --Placement of precast sporidia onto pine has resulted in successful inoculations. Sporidia are cast into water, collected on "Millipore" filters and transferred to pine tissues. Small numbers of sporidia (5 to 10) can be transferred from filters having an even distribution of spores via finely drawn glass rods. This technique has two important advantages; it provides for good inoculum density control and allows critical placement of inoculum. In addition, telial germination is separated from the inoculation technique. Although this technique is not suited to large resistance screening trials, it has promise for studies of penetration, tissue susceptibility, or inoculum density.

10. Stem insertion.--*C. fusiforme*, in the form of telia-bearing oak leaves, telial columns, and diseased gall tissue, is placed in wounds made in pine stems. Although these methods are only fairly successful, some advantage is gained via a relatively short incubation period for the formation of stem galls. This is a time consuming, unnatural method which bypasses possible needle resistance. Perhaps, stem insertion techniques could identify modes of disease resistance in the stems of trees immune due to foliar resistance factors. These "bark resistant factors" which, otherwise, would be masked by resistance to initial establishment of the fungus could provide for the establishment of useful differentially resistant lines.

11 and 12. Injection of sporidia into pine stems and needles.--Sporidia collected on water beneath germinating telial columns, centrifuged, and drawn into a syringe are injected into pine tissues. Both stem and needle tissues can be inoculated in this manner. Because inoculum of varying densities can be placed in any desired location, this is a useful technique to study infection courts, symptom development, and modes of resistance. Insofar as disease resistance screening is concerned, obvious objections arise because injection techniques are time consuming and unnatural. Needle injections bypass mechanical plant barriers which might be involved in resistance. Stem inoculations bridge all types of needle resistance including mechanical and physiological barriers to both germination and penetration of sporidia and subsequent colonization prior

Table 2. Summary of pine inoculation techniques in *C. fusiforme* research

Inoculation technique[a]	Reference[b]	Purpose[c]	Results[d]	Advantages	Disadvantages
A. Mass Inoculation					
1. Natural inoculation	Boggess and Stahelin, 1948	effect of cultivation and fertilization on the incidence of disease (A)	good	useful to assess field resistance of many plants under varying natural conditions of site, cultural practices, climate, phenology, age of plant, stand density, etc.	no control of temperature, relative humidity, inoculum density, or time of inoculation
	Henry and Bercaw,1956	disease resistance (B, D)	good		
	Goggans, 1957	effect of year, age of tree,stand density, and species on the incidence of disease (A,B,C)	good		
	Gilmore and Livingston, 1958	effect of cultivation and fertilization on the incidence of disease (A)	good		
	Jewell, 1960a	host range of the fungus (E)	good		

		Barber, 1964	disease resistance (A)	good		
		Barber, 1966	disease resistance (B)	variable		
		Wells and Wakeley, 1966	disease resistance (B)	good		
		Wells, 1966	disease resistance (A,B,D)	good		
		Derr, 1966	disease resistance (A,C)	good		
		LaFarge and Kraus, 1967	disease resistance (A)	good		
		Snyder, Wakeley & Wells, 1967	disease resistance (A)	variable		
2.	Rust nursery	Driver, Stonecypher, and Zobel, 1966	disease resistance (A,B)	variable to be evaluated	useful to assess field resistance under natural conditions; abundant inoculum in close proximity of pine; some ability to maintain high relative humidity	little control of temperature or inoculum density; no interactions with site when restricted to one location
3.	Tent chambers over nursery beds, etc.	Jewell, 1960b	inoculation technique and symptom development (A)	good	fair maintenance of high relative humidity; abundant inoculum and control of time of inoculation	no precise control of inoculum density, temperature, or relative humidity; no site interactions

Inoculation technique[a]	Reference[b]	Purpose[c]	Results[d]	Advantages	Disadvantages
	Jewell, 1961	disease resistance (A,B,C,D)	good		
	Jewell and Mallett, 1967	disease resistance (A)	good		
4. Screening shed	Jewell (unpub.) and Dinus (unpub.)	disease resistance (B)	good	good maintenance of a moisture saturated atmosphere; some temperature control	difficult to control inoculum density; time required to handle seedlings is considerable
	Goddard and Schmidt (unpub.)	disease resistance (A)	to be evaluated		
5. Inoculation chambers	Kinloch, 1968	disease resistance (B)	variable	fair maintenance of a saturated atmosphere and some control of temperature	difficult to control inoculum density
	Dwinell, these proceedings	disease resistance, epidemiology	good	control of inoculum density, temperature, and relative humidity	chamber is complex and small for use in mass screening studies
	Blair (unpub.)	disease resistance	good		
	Schmidt (unpub.)	effect of dew on germination and penetration of sporidia (A)	to be evaluated	control of amount and duration of dew and temperature and relative humidity	difficult to control inoculum density, also small and complex

B. Individual Tree Inoculations					
6. Telia suspended above individual seedlings	Hedgcock and Siggers, 1949	fungus taxonomy and host relationships (A,B, C,D,E)	fair	probability of each plant receiving abundant inoculum on susceptible tissue is high	difficult to control inoculum density; time required in large studies is considerable
	Jewell, 1960b	inoculation technique and symptom development (A)	fair to good		
	Goddard and Arnold, 1966	disease resistance (A)	good		
	Kinloch and Kelman, 1965	disease resistance (B)	good		
	Roncadori, 1965	pathogenicity of secondary sporidia (A,B)	good		
	Kais, 1966	persistance of albino form (A)	good		
	Patton and Johnson, 1966	penetration of pine needles by sporidia (A)	good		
7. Inoculation chamber	Snow, 1968b Snow and Kais, these proceedings	time required for infection of pine (A)	good	good control of inoculum density, temperature, and relative humidity	single plant capacity, recalibration of chamber to regulate spore density

Inoculation technique[a]	Reference[b]	Purpose[c]	Results[d]	Advantages	Disadvantages
8. Water suspensions of sporidia	Jewell, 1960b	inoculation technique and symptom development (A)	negative	a convenient method which allows some control of inoculum density and placement of inoculum	results have been negative or quite variable
	Hare, these proceedings	mechanism of disease resistance (A,B,D)	negative		
	Miller (unpub.)	inoculation technique, symptom development (A)	variable		
9. Direct placement of precast sporidia onto pine tissues	Miller, in press	penetration, colonization(A)	good	good control of inoculum density and placement of inoculum	only one plant can be inoculated at a time
10. Stem insertion	Hedgcock and Siggers, 1949	fungus taxonomy and host relationships (A,B, C,D,E)	fair to good	shorter time required for stem gall formation, useful to disclose bark resistance factors	a time consuming unnatural method which negates any type of foliar resistance or stem resistance imparted by a mechanical barrier
	Jewell, 1957	inoculation technique	poor		
	Jewell, 1960b	inoculation technique and symptom development (A)	fair		

	Arnold and Goddard, 1966	disease resistance (A)	fair		
	Kais, 1966	persistance of albino form (A)	good		
11. Injection of sporidia into pine stems	Hare, these proceedings	mechanism of disease resistance (A,B,D)	good	same as above plus the ability to place inoculum in different parts of the stem	
12. Injection of sporidia into pine needles	Powers, 1968	symptom development (A)	good	ability to place inoculum on different needle types and needle locations	unnatural, time consuming method which negates any foliar resistance to germination and penetration
	Hare, these proceedings	mechanism of disease resistance (A,B,D)	good		

[a] The number of the technique corresponds with that in the text.

[b] Unpublished references were obtained by personal communication.

[c] A = slash pine; B = loblolly pine; C = longleaf pine; D = shortleaf pine; and E = other.

[d] Results refer only to the inoculation success, not to the purpose of the study; if the objectives of the study were fulfilled the results were considered good.

to gall formation. As mentioned previously, stem injection techniques could be useful in studies of bark resistance factors and differential resistance types.

INOCULATION OF OAK

Artificial inoculation of oak with aeciospores of *C. fusiforme* is less demanding than the sporidial inoculation of pine and is easily accomplished in the laboratory or field. Usually fresh or stored aeciospores are dusted onto the wetted, lower surface of susceptible oak leaves. Optimum temperature for germination of aeciospores is approximately 20°C (Siggers, 1947; Roncadori and Matthews, 1966). Most critical, however, is the age of the oak leaves; maximum uredial and telial formation occur on leaves inoculated at 4-6 and 8-12 days of age, respectively (Snow and Roncadori, 1965).

DISCUSSION AND CONCLUSIONS

Problems associated with inoculation techniques are of fundamental importance to disease resistance programs because they influence the judgment of relative susceptibility of test plants and of the mode of resistance. It is generally agreed that both artificial and natural inoculations are required(Patton and Riker, 1966; Borlaug, 1966) and that both have inherent advantages and disadvantages (Schreiner, 1966). Therefore, it is appropriate to consider how available techniques can be used best in light of present knowledge.

In regard to the development of rust-resistant pines, inoculation techniques must minimize errors of omission (a failure to identify a resistant tree) and commission (the identification of a susceptible tree as resistant). Certainly, the latter is requisite with a crop such as pine which has a rotation age of at least 20-25 years. Artificial inoculations should approximate natural inoculations and minimize chance deviations in inoculum density, availability of susceptible tissues, temperature, atmospheric moisture, and all such factors which contribute to disease escape of susceptible trees under natural conditions. Likewise, natural inoculations should aid in the interpretation of geographic interaction due to climate, pathogen, or host variation, effects of cultural treatments, stand manipulation, and such factors which are difficult to include in artificial inoculations.

With respect to fusiform rust, a feasible inoculation routine which accomplishes many of the above objectives would include: (1) mass artificial inoculation of 1-3 month-old seedlings in screening sheds using mixed inoculum, i.e., inoculum which samples possible existing racial variation in the fungus, (2) reinoculation of these seedlings at age 1-3 years, using mixed inoculum in tent-chambers over nursery beds, and (3) field testing of promising individuals for 3-5 years in rust nurseries strategically located to test geographic interaction. The latter should be a joint regional effort wherein cooperators would accept test material from other areas. A similar plan has already been outlined for white pine blister rust (Borlaug, 1966). If pines are to be used only locally more intensive tests with only local inoculum might be appropriate.

Results from recent studies of *C. fusiforme* which support the above approach are: (1) the possible existence of racial variation in the pathogen (Snow, Powers and Kais, 1969), (2) in the field, significant differences between 3 and 5 year rust ratings occur (LaFarge and Kraus, 1967), and (3) preliminary data indicate a close agreement between artificial (screening-shed) and natural inoculations with regard to relative susceptibility of test trees (Dinus, 1969 and this proceedings).

Although this intensive screening procedure appears feasible, it is designed to detect only a "supertree", i.e., one that is resistant at age 1 month through 6 years to different sources of inoculum and on a variety of sites. Because screening-shed inoculations subject very young seedlings to high levels of inoculum, we might be discarding seedlings that would be resistant at an older age when they are normally exposed to the fungus in the field. After all, we can protect young seedlings in the nursery. If resistance increases with age, perhaps more emphasis should be placed on steps (2) and (3) above. In regard to field testing, we know from the seed source studies that some sources perform best in given areas and, therefore, probably will not be planted on all sites. Is it realistic to test this material over a large range of sites?

A most important consideration in any rust resistance program and one that is related directly to inoculation technique and evaluation of the results is that of horizontal versus vertical resistance. Assuming racial variation in *C. fusiforme* exists, it would be a mistake to utilize a selection scheme that would overlook or discard horizontal resistance. For, unless a phenomenon such as "stabilization selection" (van der Plank, 1968) is operating in the forest and can be utilized, there are obvious dangers involved in the management of plantations containing only one or several vertically resistant trees. Although with existing heterozygosity and open pollinated seed orchards, pine genotypes will probably not become as homozygous as other agricultural crops.

A critical question in any consideration of inoculation techniques is that of the effect of inoculum density on disease development. The relationship between numbers of sporidia and numbers of foliar lesions and subsequent stem galls needs clarification in respect to genetic and environmental variability. This information would be of primary importance to individuals investigating disease resistance, especially those concerned with screening programs.

At present, the best selection criterion for fusiform rust resistance is the number of cankers per infected tree (Goddard and Strickland, 1966; LaFarge and Kraus, 1967). These authors found a significant positive correlation between the number of cankers per infected tree and the percent of diseased trees within progeny lines. Needle symptoms are not always indicative of subsequent gall formation. Resistant shortleaf pines (*Pinus echinata* Mill.) develop needle symptoms but no galls (Henry and Jewell, 1963; Jewell, 1966; Hare, these proceedings). Possibly, resistant varieties of slash pine (*P. elliottii* Engelm. var. *elliottii*) or loblolly pine (*P. taeda* L.) would react in a similar manner. To the contrary, susceptible slash pine seedlings can develop cotyledonary symptoms without subsequent gall formation (Powers, 1968); this further complicates the use of foliar lesions as an indication of resistance.

In closing, I would emphasize that a greater effort should be made to select fusiform rust-free trees from plantations and natural stands where the incidence of rust is high. At present, many of the candidates in our tree improvement programs were selected primarily on growth parameters and/or from areas of relatively low rust incidence. These trees probably represent a population with a high percentage of disease escapes rather than resistant individuals.

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FLOOR DISCUSSION

(Also discussed here are three previous papers in this panel section by Snow and Kais, Dinus, and Dwinell covering *C. fusiforme* inoculation problems and techniques.)

WEISSENBERG: For my personal interest, I'd like to hear commentary on the influence of age of telial columns on basidiospore density.

DWINELL: The work of Powers and Roncadori indicated that there was a direct relationship between telial age and sporidial cast. This was the reason we used 2-week-old telia; at that age they produce the maximum sporidial cast.

GERHOLD: I have gathered from some of the comments that density of basidiospores in the nursery bed type of inoculation is rather variable, that is, that the number of spores per seedling might vary even across small areas. Would it be possible to adapt some of the more sophisticated inoculation chambers, like the one developed by Dwinell, for use in the nursery. I'm thinking of a mobile unit that travels down the nursery bed, perhaps with some sort of spore distribution system using a manifold.

DWINELL: I really don't know if we need such close control for mass or screening inoculations in the nursery. Instead I think we need basic information on the relation of inoculum density to infection. By knowing spore density in the screening test, and what that density means in respect to infection, we might be able to get along very well. However, we're not at the point yet where we are involved in a mass screening program. We will have to consider these problems once we reach that point.

KINLOCH: Dr. Schmidt, what is the range or limitation of temperature control in your screening shed? Is this a limiting factor?

SCHMIDT: In our studies in Florida temperature control has not been too much of a problem. We control relative humidity by spraying water on the canvas sides of a large screening shed. Coincidentally we get evaporative cooling, and this maintains the temperature around the 70°F optimum even when outside temperature is 80°F and above. Thus temperature control hasn't been a problem with the screening shed.

ARTIFICIAL INOCULATION OF LARGE NUMBERS OF *PINUS MONTICOLA* SEEDLINGS WITH *CRONARTIUM RIBICOLA*

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ABSTRACT

Methods used at the author's laboratory in northern Idaho for simultaneous, artificial inoculation of up to 75,000 young *P. monticola* seedlings in blister rust resistance, progeny test nursery beds were described and illustrated. Problems of securing heavy and uniform inoculation were discussed. We have obtained heavy but spotty inoculation, and thus lack of uniformity continues to be a costly problem.

Delayed germination common in *P. monticola* seedbeds resulted in 1- and 2-year-old seedlings in most row-plots. In tests conducted during two successive years all seedlings in each test were inoculated simultaneously in a single 72-hour period, when seedlings that had germinated the first growing season were 2 years old. The seedlings were examined for foliar lesions approximately 1 year after inoculation and for bark lesions approximately 2 years after inoculation. Compared with the 2-year-old seedlings, within 85 full-sib progenies of the first test, 11% more of the 1-year-old seedlings had foliage infections; 28% more had bark infections. Within 97 full-sib progenies of the second test, corresponding results were 20 and 48%.

INTRODUCTION

Since 1950 the Intermountain Forest and Range Experiment Station and the Northern Region--both of the Forest Service, U. S. Department of Agriculture--have been cooperating in a program of research and development toward mass-production of western white pines (*Pinus monticola* Dougl.) that are resistant to blister rust (*Cronartium ribicola* J. C. Fisch. ex Rabenh.). This work necessitated an increased capacity of inoculation chambers from that required for inoculating a few thousand seedlings in portable flats up to that sufficient for simultaneous inoculation of more than 75,000 seedlings planted in 800 running feet of 4-foot-wide nursery beds (almost 1/8 acre) (Fig. 1). Meanwhile, with greater or lesser success, we have attempted to increase intensity of resulting infection and control the uniformity of inoculation.



(A)



(B)

Figure 1. Inoculation chambers: (A) Earlier version, inner walls and shading of canvas, covering 3,000 seedlings in one run (Spokane, Washington, 1953); (B) Present version, inner walls of 6-mil polyethylene film, shading of canvas, covering 75,000 seedlings in one run (Moscow, Idaho, 1966).

PROGENY TEST DESIGNS

EARLY TESTS

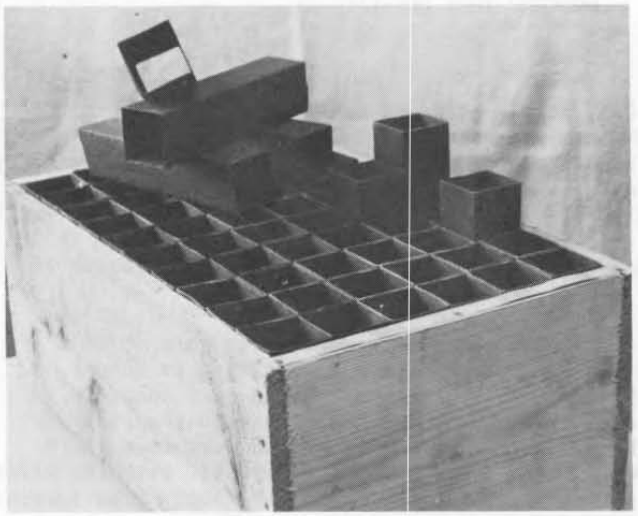
Between 1950 and 1953, at the start of our work on blister rust resistance in western white pine, we pollinated to the limit of female flowering on available candidate trees (i.e., rust-free or phenotypically resistant trees selected in heavily infected natural stands). This kept us quite busy, but resulted in a very irregular mating scheme among full-sib seed progenies that were scheduled to be sown, inoculated and examined in a given progeny test. Some tests included 20 progenies of one candidate, and only one or two of another candidate.

The 30 to 100 full-sib seed progenies produced per year in this period were stratified during winter and sown each spring in annual progeny tests between 1952 and 1955. Tests consisted of 9 complete randomized blocks with each progeny represented by one 10-seedling row plot replicate per block. Seeds for a given row-plot were sown in 10 2"x2" tar paper plant bands, 6 row plots per flat (Fig. 2), with the flats then plunged, back-to-back to ground level, in nursery beds. The largest of these four tests contained about 9,000 seedlings. These were inoculated at 2 years of age, in three successive inoculation runs of 3,000 seedlings each. Canvas inoculation chambers were used in the shade of canvas flies (Fig. 1A).

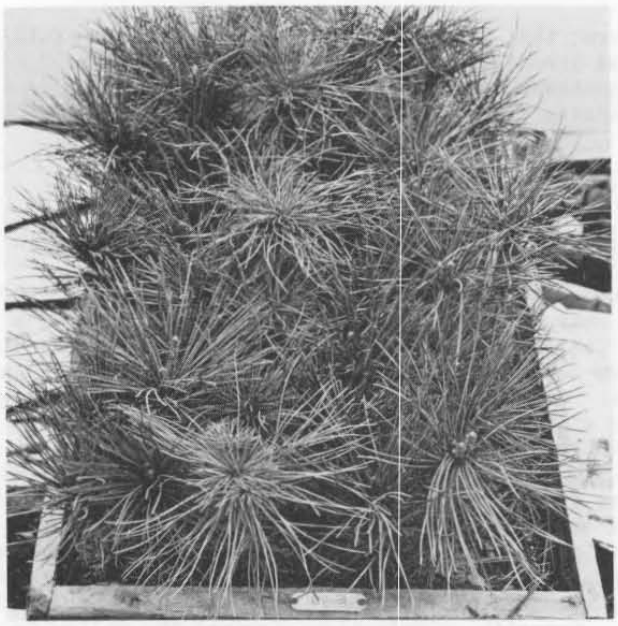
It soon became apparent that the mating design, the canvas inoculation chambers, and several inoculation runs of the early tests were unsatisfactory. The fragmentary mating design often left us quite puzzled as to which candidates transmitted useful levels of resistance.

RECENT TESTS

In tests sown from 1960 on we increased the number of seedlings in each row-plot to 16, and the number of blocks to 10. Also, we used a tester-mating scheme wherein each candidate was crossed with four tester trees. Because of these improvements and the increased efficiency of a larger pollination crew, test size increased markedly. The seed progenies sown each year ranged from 160 to 475 and occupied from 200 to 800 running feet of nursery bed space. We no longer had time nor money for handling plants in plant bands and flats, or for stratifying the many different seed lots; instead, in the fall we presowed seed for each progeny on a drop of methyl-cellulose mucilage (with "Captan" fungicide added) placed on stenciled seed planting spots on paper-towel strips (Fig. 3A). Length of each strip was equivalent to 10 3"x24" row-plots (Fig. 3B). Each of these 10-row-plot seed strips (replicates) was cut apart and prerandomized for planting the 10 blocks. Each 3"x24"strip was then simply laid on the surface of the bed at the correct row and block position and covered with 1/4" of plasterer's sand. Normally, germination occurred the following spring, and tests were inoculated either that same fall when earliest germinating seedlings were 1 year old or the following fall when they were 2 years old.

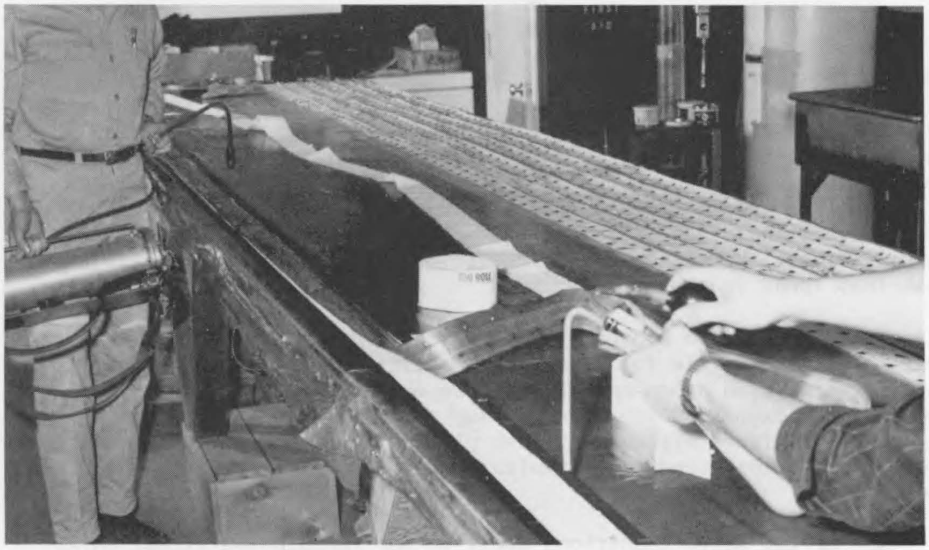


(A)



(B)

Figure 2. Tarpaper plant bands, 60 to the flat, as used in early progeny tests: (A) Before sowing; (B) Showing 2-year-old seedlings at time of inoculation. The small seedling immediately above and to the right of the flat tag would be scored as 2/8*th* "screened", i.e., overtopped by foliage of the two larger seedlings on its right and left.



(A)



(B)

Figure 3. (A) Presowing progeny test seed on paper toweling strips; left, stenciling seed spots, right front, placing methyl-cellulose droplets on stenciled seed spots in which seed are sown; rear, drying the presown, 10-block strips. (B) The 3"x24" toweling strips are randomly fall-sown in seedbed compartments and covered with sand; after germination they become the basic 16-seedling replicates of the test.

PROBLEMS OF LARGE-SCALE INOCULATION

CONTROLLING TEMPERATURE AND HUMIDITY

To inoculate more than a few thousand seedlings the researcher usually must use artificial inoculation in outdoor nurseries where young seedlings are compacted in nursery beds or portable flats. For convenience and accessibility, and to reduce time and costs of all progeny test treatments and examinations, test nurseries are usually located near urban research installations. Here the environment is likely to be warmer and drier than that found in the forests.

Due primarily to weather, often there is only a short period of time available in the field for securing the best inoculum; furthermore, naturally infected *Ribes* spp. leaves are commonly the only adequate sources of inexpensive inoculum. Also, the need to secure either a heavy or at least uniform exposure of test plants requires that the investigator inoculate all test seedlings simultaneously with the same batch of inoculum.

All of the above conditions apply to our inoculation situation at Moscow, Idaho. In all of our white pine blister rust resistance progeny testing we use white pine seedling progenies in a small and highly specialized nursery. Knowing that this nursery was relatively warm and dry, we delayed our first large-scale inoculations until the nursery environment had cooled. Then, because of frosts, we were often too late to collect the preferred inoculum--solidly-infected *Ribes hudsonianum* Richards var. *petiolare* (Dougl.) Janz. leaves from this large-leaved, streambottom plant. Instead, the less heavily infected leaves of upland *Ribes* spp. (principally *R. viscosissimum* Pursh.) were used; these upper-slope plants were protected from frost by the warm air of a hillside or a ridge-top temperature inversion zone (see Mielke, Childs and Lachmund, 1937, for relative susceptibility of these *Ribes* spp.).

Fortunately, a really hot early October inoculation season finally occurred. In the second and third days of the 72-hour inoculation period, temperatures in the inner inoculation chambers reached 85°F , and relative humidity dropped below 95%. Thus, temperatures exceeded the 50-65°F range reported as optimal in the eastern and central U.S.A. for *C. ribicola* teliospore germination, for production and germination of basidiospores, and for penetration of pine needles by the germ tubes thereof (Hirt, 1935; Van Arsdel, 1954). In fact, the supposed maxima (approximately 70°F , Hirt, 1935) for teliospore and basidiospore germination were exceeded. On two occasions the relative humidity dropped below the supposed critical level of 97% (Hirt, 1935); but despite this, standing water was maintained on some pines and *Ribes* spp. leaves for at least two 12- to 16-hour periods of presumably near optimal conditions (50-60°F , 100% R.H.) that occurred overnight. Even with these conditions, after 2 years control seedlings were 85% infected.

As a result of these experiences we commenced inoculating earlier in the season, i.e., from September 10 to 20 when higher quality *R. hudsonianum* inoculum was available. In the last several years we have inoculated during seasons when outside, mid-day temperatures exceeded 95°F and inner chamber temperatures 87°F , with relative humidities below 85%. Two years after inoculation we have found control plants 75 to 100% infected. Thus, we can make highly successful, simultaneous inoculations of large progeny tests given: (1) fairly spacious chambers (approximately 8 to 10 cu ft

of air space per sq ft of ground space) which when thoroughly soaked have fair capacity to withstand sudden rises in temperature without corresponding drops in relative humidity; (2) hand misting during critically warm periods; (3) good inoculum; and (4) a 72-hour inoculation run including 12- to 16-hour periods where near optimal conditions are maintained.

VARIATION IN INTENSITY OF INOCULATION

Results from inoculating almost 80 different, control lots (presumably non-resistant seedlings) over 11 different seasons are given in Table 1.

It is interesting that Control RR, used in four different seasons, is the least infected (75-96%) control during the four seasons in which it was used. The seed came from a residuum of seven infected trees in a very heavily infected natural stand where most western white pines were already dead or dying. The seedlings were partly resistant.

The year-to-year variation in infection we have experienced following inoculation of 2-year-old plants ranged from 75 to 89% following inoculation of 1-year-old plants the variation of infection ranges between 76 and 99% (see Table 1, column 8). This is a fairly wide variation, but the over-all level is certainly adequate for progeny testing if the number of seedlings and replicates per progeny is kept large.

There was no obvious relationship between number of basidiospores trapped per sq mm (in 72 hours on vaseline-coated slides placed at seedling level in center of inoculated seedbeds) and the intensity of infection of control seedlings. Estimating that a 2-year-old seedling had 400 lineal cm of secondary needles, 1 mm wide (a 4,000 sq mm target), then according to the spore-cast data of columns 5 and 6, Table 1, the interception of sporidia by a 2-year-old seedling would range between 11,000 and 48,000 sporidia, with 3,200 to 9,600 of these spores known to be germinable. Corresponding estimates for 1-year-old seedlings with 100 lineal cm of primary needles and cotyledons (1,000 sq mm target) would be 3,700 to 12,500 sporidia intercepted per seedling with 1,400 to 3,200 germinable spores. It was indeed surprising that variation in degree of infection did not accompany such 3- to 4-fold increases in exposure, sometimes involving differences of tens of thousands of sporidia per plant. Other environmental factors inside the inoculation chambers must have exerted over-riding influences.

VARIATION IN UNIFORMITY OF INOCULATION

While we may have consistently secured heavy infection of susceptible control plants, we still have serious problems securing *uniform* inoculation throughout any large experiment where several nursery beds are inoculated simultaneously.

In our earliest inoculations (1953) we were using canvas inner and outer inoculation tents that straddled two nursery beds, along with continuous misting from a line of nozzles suspended over the aisle between the beds (Fig. 4). Apparently, we were floating away basidiospores collected on foliage of the inner rows of seedlings nearest the nozzle line, yet allowing other basidiospores to dry and die on seedlings in the outer rows near the drier canvas wall. Seedlings in portions of these inner and outer rows (including some controls) averaged only 35 to 55% infected, while infection in five control lots of the same test averaged 77%.

Table 1. Variation in percentage of control plants infected in different inoculation seasons

Year inoc.	Seedling age	No. of lots inoc.	No. seedlings inoc.	Basidiospore casts		No. yrs. after inoc. insp.	Av. % seedlings infected[a]	Range in % infection in lots	Control lot having lowest % infection	
				Germinating	Total				Lot	Source
				(spores/sq mm)						
1953	2	5	429	---	---	2	77.1	64-86	E	Commercial, squirrel cache, probably from many mature trees
1954	2	4	274	---	---	2	89.0	82-99	F	7 cones from 6 infected trees from heavily infected pole stand
1955	2	4	241	---	12.0	2	74.9	68-85	N	5 cones from each of 6 infected trees in med.-heavily infected pole stand
1956	2	8	438	---	5.8	2	87.3	64-96	W	11 cones from each of 2 infected trees in heavily infected pole stand
1958	2	5	1862	---	---	1	80.5	79-82	Y	Mix of 30 cones from squirrel cache in heavily infected pole stand
1961	1	10	1124	1.7	10.2	2	75.9	50-93	KK	5 cones from each of 5 infected trees, same area as control Y
1962	1	7	950	2.4	7.9	2	99.6	98-100	TT	6 cones from each of 6 infected trees in heavily infected pole stand
1963	1	6	744	0.8	2.8	2	96.9	96-98	RR	5 cones from each of 7 infected trees in in heavily infected pole stand
1964	1	6	1062	2.4	7.9	2	94.5	90-98	RR	Ditto
1966	1	8	148	1.4	3.7	1	89.2	75-100	RR	Ditto
	2	10	1450	1.4	3.7	3	88.0	80-96	UU	6 cones from each of 5 infected trees same area as lots Y & KK
1967	1	5	995	3.2	12.5	1	96.0	92-98	RR	(above)
	2	5	680	3.2	12.5	1	86.6	77-92	ZZ	7 cones from squirrel cache in moderately infected pole stand.

[a]Infected seedlings supported typical needle and/or bark lesions.



Figure 4. Early inoculation tests using vegetable-bin mist sprayers suspended above and between two nursery beds. The inoculum consists of infected *Ribes viscosissimum* leaves, still on the bushes, with the freshly cut stems merely plunged into the moist soil.



Figure 5. Standing water maintained on seedlings by intermittent hand misting. The paper barrier in the foreground is an attempt to curtail edge drying.

Some improvement was obtained by: using inner chambers of polyethylene film; protecting outer rows of seedlings with paper or wet burlap barriers to prevent drying; maintaining standing water droplets on seedlings by intermittent, hand misting (Fig. 5); and using *R. hudsonianum* leaf rather than *R. viscossimum* bush inoculum. Despite these improvements, given a really large test involving several contiguous chambers and a warm inoculation season, fluctuations in levels of infection within and between the chambers have remained large. For instance, in 1966 when 800 running feet of nursery beds containing more than 75,000 seedlings were inoculated in three large, contiguous chambers (Fig. 1), it required almost 8 hours for a 6-man crew to lay out infected *R. hudsonianum* leaves on screens suspended above the seedbeds (Fig. 6). The first of three chambers on the east was "buttoned up" at 10:00 a.m. and the last on the west at 3:00 p.m., by which time some of the succulent *R. hudsonianum* leaves were wilting. During this inoculation ambient air temperatures reached 95°F, inner chamber temperatures 87°F. On the warmest afternoons a 3-man crew simply could not move fast enough with hand-mist nozzles to maintain water droplets on all seedlings. This is not surprising when one considers that at 50°F a cubic meter of saturated (100% R.H.) air contains 9-1/2 gm of water, while at 86°F it contains 30-1/2 gm--or 3-1/4 times as much. Despite these problems, 3 years after this single, 72-hour inoculation, average level of infection in 10 "non-resistant" control lots of the main experiment was 88% (Table 1).



Figure 6. Infected *Ribes hudsonianum* leaves being laid out on inverted nursery bed cover screens, approximately 18 inches above pine seedlings. Leaves from five or more different *Ribes* bushes are systematically mixed during this process.

The likely source of our problem is apparent from a look at variation in infection intensity across a large test, as diagrammed in Figure 7 1 year after inoculation. There seems to be an obvious association of position of seedlings with degree of infection, especially along the extreme east and west walls, and along the south walls of the three continguous inoculation tents. Apparently overheating and drying are still problems to be reckoned with.

These fluctuations are creating relatively high variances between the blocks and they explain why we use both a relatively large number of replicates (10) and seedlings (160) for each test progeny. Effects of this variation are discussed elsewhere in these proceedings by Becker and Marsden.

Levels of rust infection diagrammed in Figure 7 held 1 year after inoculation; they were based mainly on needle lesions. Drs. McDonald and Hoff of this Laboratory point out that because of the length of time (50 days, September 1-October 20) required to move across the main test (below the dotted line of Figure 7); moving from east to west, the lower infection on the west may be partly of an artificial nature. They suggest this because when they sampled blocks 4-7 in mid-June they found foliage lesions on 99.6% of the sample seedlings. Yet when we reexamined the seedlings of the same four blocks 3 months later in mid-September the infection was much lower (see Blocks 4-7, Figure 7). McDonald also found that premature shedding of infected needles is a resistance trait that is under monogenic control (McDonald, 1969). We know that during warm seasons some infected foliage begins dying and becomes unrecognizable as such by early July.

PLANT SIZE IN RELATION TO SUSCEPTIBILITY

Starting with our earliest inoculations we noticed the relatively low intensity of needle spotting in certain small, slow-growing, and apparently low-vigor seedlings and progenies. Some of these runty seedlings were transplants, replacing missing plants; others were located in under-fertilized portions of seed beds, and still others were from late germinating seed or in self-pollinated progenies. In one progeny test, simple correlation of number of needle infections on a 1,715 lineal cm needle sample with average progeny height (2-year-old seedlings) showed that needle lesion frequency was significnalty, if not strongly, correlated with progeny height ($r = .403$, significant at the 5% level). Regression coefficient, "b", was roughly 430 needle spots per 1,715 lineal cm needle sample, for each additional cm of plant height.

And, as expected in the same test progeny (Squillace and Bingham, 1958) seed weight was also significantly, if not strongly associated with average progeny 2-year-old seedling height ($r = .426$, significant at the 5% level, $b = .00025$ cm of height for each mg of seed weight). Would it be necessary to adjust observed needle-lesion-intensity values for the extraneous height variation associated with variation in seed weight? For practical purposes, the adjustment proved to be unnecessary. Average progeny seed weights seldom ranged 100 mg from the mean (230 mg). Even if they were that far from the average, the increment of seedling height due to seed weight would have been relatively small (i.e., 100 x .00025 cm = 0.025 cm height); and this small increment of height would produce a small change in number of spots per 1,715 lineal cm needle sample (i.e., 0.025 x 430 spots = 11 spots, while the average progeny had about 200 spots per 1,715 lineal cm needle sample).

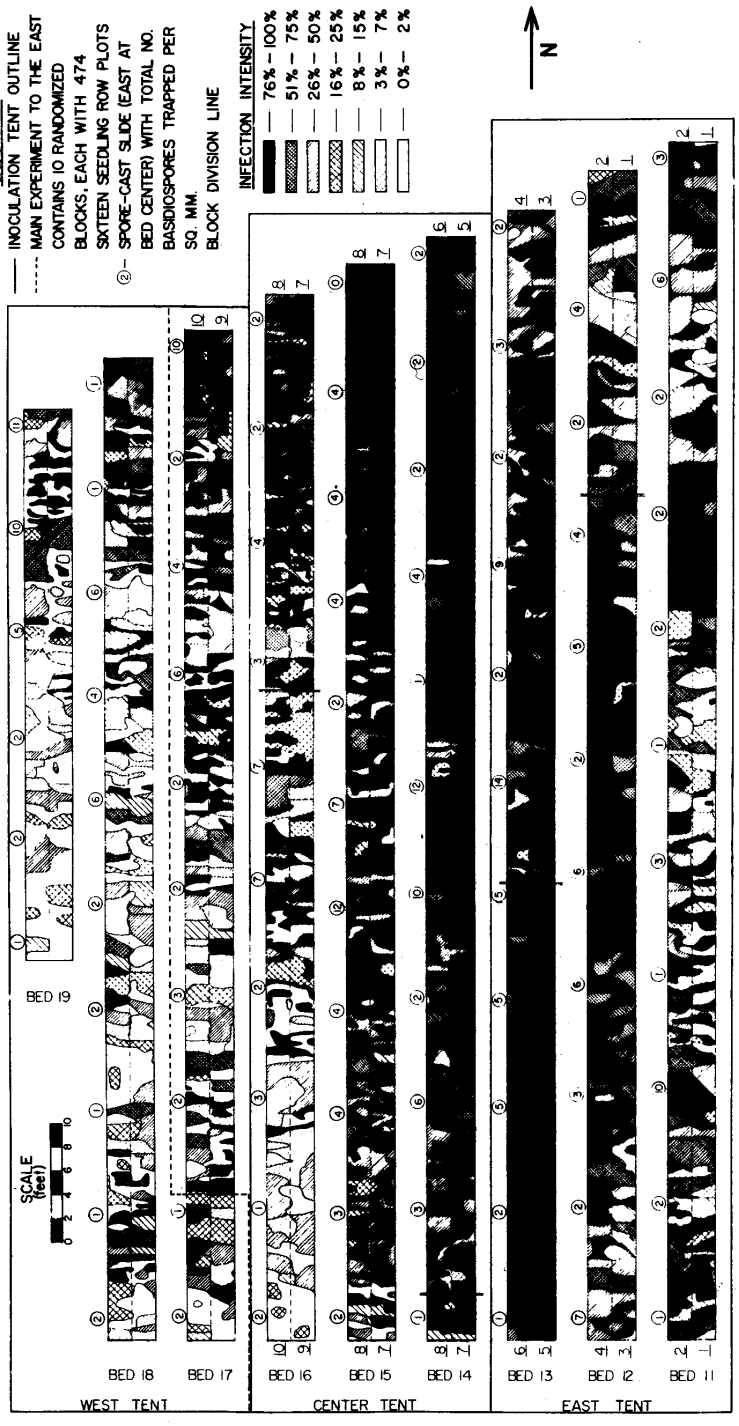


Figure 7. Infection intensity one year after a single, 72-hour inoculation of 800 running feet of nursery beds (75,000 seedlings) in 1966.

Remaining differences in progeny average heights were considered to be male, female, or male x female effects (i.e., genetic), so adjustments of observed needle-lesion values for variation in seedling height were not attempted.

Another indirect effect of plant height on infection, especially where seedlings grew quite close together when inoculated, could be the interception of basidiospores falling from above (screening) by foliage of the larger and taller adjacent plants (Fig. 2B). However, in the experiment examined, partial correlation analysis showed that intensity of foliar infection, independent of screening, was again significantly correlated with 2-year-old seedling height ($r = .430$, 5% level). Screening itself (scored 1/8*th* for each of the overtopping adjacent seedlings, see Fig. 2B), however, independent of height, had no significant effects on spotting intensity.

PLANT AGE RELATED TO SUSCEPTIBILITY

For some time now it has been recognized that resistance of white pines increases directly with host age, at least up to the age of 4 years (Heimburger, 1958; Patton, 1961; Patton and Riker, 1966; Bingham, *et al.*, 1969). Thus, difficulties occurred when we attempted to reduce test time by inoculating the 1-year-old instead of 2-year-old seedlings. In fact, we practically decimated some tests where we had inoculated extremely susceptible 1-year-old seedlings. Seedlings of the most resistant 1-year-old progenies survived at levels barely discernible above controls (i.e., 5-10% versus the 25-35% usually found in tests inoculated at 2 years age).

These results on 1-year-old seedlings caused us to quit inoculating progeny tests the first fall after sowing. Nevertheless, because of the severe dormancy problems of *P. monticola* seed, we are still faced with the age problem. In all progeny tests inoculated at a seedling age of 2 years, 20 to 50% of the germinable seed simply fail to germinate the first spring after sowing. They germinate a full year later, so that our tests are always confounded by the presence of both 1- and 2-year-old seedlings.

The year's delay in germination is often strongly associated with progenies of certain mother trees; but late sowing (November or December) of the normally October-sown seed definitely increases the problem in all seed lots. The only advantage of this situation is the weighty data provided on the difference in susceptibility of 1- versus 2-year-old seedlings.

A comparison of infection in seedlings either 1 or 2 years old when inoculated was possible within full-sib progenies of several progeny tests. In two of the largest tests (1964 and 1965), an analysis of infection was made in all progenies having 20 or more seedlings of both ages, where those seedlings occurred in at least 5 of the 10 randomized progeny row-plots of the test. Results are shown in Table 2.

It can be seen that in the 1964 test, 11% more of the 1-year-old seedlings bore needle lesions, and 29% more bore bark lesions than did the 2-year-olds. Similarly, in the 1965 test, 20% more of the 1-year-olds bore needle lesions, 48% more bore bark lesions. The control seedlings exhibited less difference in infection between 1- and 2-year-old plants. One-year-olds were only 3 to 13% more heavily needle spotted, or 11 to 28% more heavily cankered than the 2-year-olds.

Table 2. Difference in degree of infection one year after simultaneous inoculation of 1- and 2-year-old seedlings of identical full-sib progenies

Year of progeny test[a]	Year test inoc.	Year of rust exam.	Tot. No. full-sib progenies	Tot. No. diff. parents	Total No. seedlings examined		Av. % infected				Control infection				
							With needle lesions		With bark cankers			Av.% with foliar infec.		Av. % cankered	
					Age 1 at inoc.	Age 2 at inoc.	Age 1	Age 2	Age 1	Age 2	No. con-trol lots	Age 1	Age 2	Age 1	Age 2
1964	1966	1967	85	43	3383	4585	83	72	57	28	10	88	85	70	59
1965	1967	1968	97	40	8028	7492	94	74	84	36	6	96	83	83	55

[a] *Progeny tests were sown in the late fall of the test year; thus, the oldest seedlings germinated the following spring (1965 or 1966) and the younger seedlings in 1966 or 1967.*

These differences in susceptibility were quite remarkable, especially when one considers that in intercepting basidiospores a 2-year-old seedling presents 4 times the "target" of a 1-year-old. Possible explanations of this higher resistance of older seedlings are that: (1) stem as well as primary foliage infections may occur on 1-year-old plants (Van Arsdel, 1968); and (2) the primary needles lack a resistance mechanism known to be present in the short shoot, or fascicle base, of secondary foliage (unpublished data, this laboratory).

SUMMARY

In the course of 15 years work at this laboratory we have artificially inoculated more than a million *P. monticola* seedlings with *C. ribicola*. We can say that our efforts to secure heavy infection have been quite successful, but in the same breath we should admit that we are still far from obtaining a degree of control of the inoculation process that will permit us to secure uniform infection. Consistently we have obtained heavy (average 85%) infection of control seedling lots. But the between-block variation in inoculation and infection in these, or of the full-sib, test-cross lots comprising the progeny test, is forcing us to use relatively large numbers of seedlings per replicate, and large numbers of replicates per progeny. Substantial savings are possible if we can control uniformity, as well as intensity, of inoculation.

Seedling height is significantly associated with the frequency of blister rust lesions on western white pine seedling needles, but except for a small increment of seedling height due to seed weight, effects are parent associated. Seedling age, as already reported for both *P. strobus* and *P. monticola*, has a strong effect on degree of infection.

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FLOOR DISCUSSION

Panel leader Patton withheld floor discussion so that this paper could be discussed along with his own closely related paper, immediately following.

INOCULATION METHODS AND PROBLEMS IN TESTING EASTERN WHITE PINE FOR RESISTANCE TO *CRONARTIUM RIBICOLA* [1]

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ABSTRACT

Essentially the methodology used in testing eastern white pine for resistance to *Cronartium ribicola* is relatively simple, but the major problem remains of obtaining severe and uniform infection. Natural inoculation may be incorporated in progeny testing programs, but little control can be exerted over this except for site choice and preparation and the possible increase of inoculum in the area. Artificial inoculation methods are classed as spore casts, spore suspensions, and infected-tissue grafts. Spore cast methods have been successful, but lack the refinement of standardization or control over amount of inoculum applied.

An adequate supply of inoculum is essential, and this has been guaranteed to a limited extent by the development of ribes gardens of leaf-retaining strains of *Ribes nigrum*. So far dependence has been entirely on freshly-collected inoculum, and reliable methods of storage of telia or of basidiospores have not been developed.

Emphasis is given to the fact that each stage of development in the series of activities encompassed by inoculation requires different environmental conditions. These various external influences may affect the efficiency and reliability of inoculation. Age of stock is one factor that is under the breeder's control. Also, fluctuating temperatures within the range of about 4 to 21°C are known to favor infection through stimulation of infection structure formation.

The major problems at present relate to lack of standardization of inoculum and the inability to relate quantitatively host response to amount of inoculum. Improvement in present methodology may come from a better understanding of factors influencing the infection process and from development of better methods of applying inoculum.

[1] *Published with the approval of the Director, Wisconsin Agricultural Experiment Station. Experience and results of the author reported here have come from investigations supported in part by the Wisconsin Department of Natural Resources (formerly Wisconsin Conservation Department), National Science Foundation Grant GB-3297, and U. S. Forest Service Grant No. 1 (4000).*

INTRODUCTION

In a program of breeding for resistance, providing a broad base of exposure to the pathogen in the testing phase can be as important as providing a broad base for initial selection of the suscept. The testing stage must include the wide range of virulence exhibited by different strains of the pathogen, as well as providing favorable conditions for infection and disease development to insure as severe and uniform exposure as possible. Here are included such steps as learning how to create a localized epidemic in the experimental field or nursery, locating test plots at such places where the environmental factors are conducive to an epidemic outbreak, and manipulating cultural conditions to increase chances for infection.

In developing strains of white pines resistant to the blister rust disease incited by *Cronartium ribicola* J. C. Fischer ex Rabenh., it is perhaps most important, as indicated by Borlaug (1966), to develop screening tests for progenies that will identify the best selections, the best crosses among these, and the most outstanding seedlings within these outstanding crosses. One way is to produce an artificially induced rust epidemic in the nursery. This paper summarizes some experiences with artificial inoculation in programs concerned primarily with resistance in eastern white pine (*Pinus strobus* L.) and points up some of the major problems associated with such testing. An oversimplified but nevertheless characteristic statement of the theme might be that the methods and techniques are relatively simple, but consistently obtaining severe and uniform infection is often difficult.

NATURAL VS. ARTIFICIAL INOCULATION

The use of natural vs. artificial inoculation has arguments on both sides (Patton and Riker, 1966). Probably any large-scale, resistance-breeding program will have to incorporate both procedures. Rarely, however, can natural inoculation alone be relied upon; artificial inoculation methods must be used for maximum efficiency and reliability of screening tests.

The usual pathological sequence in disease development is broken down into three successive series of activities following dispersal of the inoculum: (1) *inoculation* - the arrival of inoculum at the infection court; (2) *incubation* - the revival of activity of the inoculum at an infection court, entrance into the suscept, and initiation of disease; (3) *infection* - the subsequent activities of the pathogen, which cause progressive disease in the suscept and development of a characteristic syndrome. Most considerations of artificial inoculation include the first two of these series of activities, and this paper also deals largely with these aspects.

Certain limitations are inherent in dependence upon natural inoculation. We have relatively little control over natural inoculation except through proper choice and preparation of the test site, and perhaps also through cultural operations leading to an increase in the amount of available inoculum. Such choices and site manipulations are aided by our knowledge of etiology and epidemiology of the disease concerned. Variability in results of natural inoculation tests is constantly to be expected, however, largely because of the effect of unexpected or unknown influences.

The techniques of artificial inoculation do permit us to exert some measure of control over the course of the pathological sequence. So far only a few basic methods have been employed, and my concern here is largely with inoculation of pines, but with some reference to production and maintenance of inoculum on ribes. Besides the procedures themselves, factors influencing the success of inoculation are also considered. Many of these are factors affecting the infection process and are emphasized here, since the purpose of inoculation is to lead to infection, or a resistance reaction to it. Such factors as environmental influences and age and type of stock may be extremely important in determining efficiency and reliability of a screening test, and thus may become an absolute part of a technique.

INOCULATION METHODS

METHOD VS. TECHNIQUE

A method may succeed or fail according to the technique followed in accomplishing it. Technique connotes expertise or manner of performance, whereas a method is considered as an orderly or set form of procedure. The two terms are differentiated here not to be pedantic, but to emphasize the fact that reliability of a screening test may be quite dependent upon some of the details followed in effecting an inoculation, and upon an awareness of the differences in results that might be attained by a given method under different conditions. It is appropriate that this panel is concerned with techniques, for the factors influencing results of an inoculation procedure can be quite as important as the procedure itself.

INOCULATION PROCEDURES

Spore Casts from Telia-bearing Ribes Leaves

One commonly used method for inoculating pines is to support telia-bearing ribes leaves over the test plants by means of paper clips, toothpicks, wire or large-mesh wire screening, and enclose the test beds in cloth cages or tents. The cloth or burlap covering is sprayed with water to provide a relative humidity of about 95 to 100%, or a film of free water on the needles, and to help hold temperature within the range favorable for spore germination and pine infection for periods up to about 72 hours. Shade is sometimes provided to help maintain proper temperature and moisture conditions. This basic procedure was used successfully in the Blister Rust Nursery in Wisconsin, and in most years infection of susceptible control seedlings reached over 90% and up to 100% after such inoculations (Riker *et al.*, 1943; Patton and Riker, 1966).

Details of providing inoculum and enclosing the test beds have been modified from time to time but essentially the same basic procedure has been followed. Heimburger (1956) planted the petioles of telia-bearing ribes leaves densely in the soil among the small seedlings to be inoculated, and later placed entire shoots bearing ribes leaves into the soil close to white pine seedlings and grafts. The advantage here was that ribes leaves stayed fresh longer if not detached from the stem; often, too, shoots rooted and provided inoculum for additional inoculation the next year.

For seedbed inoculations the bed was enclosed by a frame over which wide mesh hardware-cloth screening was placed. A solid layer of ribes leaves was placed over the wire mesh and covered by burlap and lath screens. Long hose sprinklers kept the burlap constantly wet (Patton and Riker, 1966).

Greenhouse or growth-room inoculation also have been made using the same basic procedure. Generally such inoculations have been made in a mist chamber in which moisture was constantly provided as a fine mist from compressed air atomizers. For such individual tree inoculations, Van Arsdel (1968) wrapped the ribes leaf completely around the pine shoot. Enclosures of plastic films impermeable to water vapor have sometimes been used, although it has often been difficult to keep temperatures within the desired range unless they were used in a growth-room where temperatures could be closely controlled.

Most of the modifications of this basic procedure have been concerned with maintaining the moisture and temperature conditions essential to obtaining infection. Some infection has been attained on individual pine seedlings inoculated in dew chambers at Wisconsin, but the dew chambers have been less reliable so far than mist chambers or small burlap-covered inoculation chambers in which the relative humidity can be maintained at approximately 100%.

A further modification was the use by Boyer (1962) of telial columns pregerminated for 12 hours on water agar and then transferred to cotyledons and needles of small seedlings. Here, viability of telia was assured by production of basidiospores before transfer to the pines, but only about 3% infection was attained. No doubt other elements of the technique were responsible for these poor results. Otherwise, it seems that use of pregerminated telia might offer considerable advantage in reducing overall inoculation time necessary under controlled conditions of moisture and temperature.

Spore Suspensions

For securing uniform coverage of plants with inoculum and standardizing the amount of inoculum applied, the use of spore suspensions seems most appealing. As far as is known, however, such a method has not been used with any great success with *C. ribicola*. Trials with suspensions of basidiospores cast on water during an overnight period, and with telia prepared by chopping telia-bearing ribes leaves in a blender, were made in the Blister Rust Nursery at Wisconsin. Sprays of basidiospores essentially were failures while the level of infection with sprays of telia ranged from bout 35 to 50%, well below that obtained with the usual direct spore casts from ribes leaves. Examination of the trees sprayed with a suspension of telia indicated that many telia were lodged on the pine foliage and stems in drops of water and were unable to germinate because of the low oxygen level. The reason basidiospore suspensions failed to incite infection in trials both outdoors in the Blister Rust Nursery and on trees in the greenhouse is unknown. Neither method has been explored in great detail, however, and I believe some such method as this may yet have promise.

Tissue Grafts

Bark patch grafts: Where large numbers of relatively uniform stem cankers are required for experimental purposes, bark-patch grafting may be the answer. About 75% overall success with young susceptible stock was obtained by Patton (1962). Initial infection and subsequent canker development were influenced by the type and degree of resistance of the individual selection.

In patch grafting a successful "take" of the patch is not necessary for infection. The major requirement for transfer of the fungus from patch to understock apparently is contact of patch and stock over a relatively large surface area of inner bark tissues. With such a method technique is important, and the major warning that might be given novices is to avoid making cuts so deep that the cambium is exposed. This is hardly possible on stems smaller than about 5 mm in diameter. With such material it is advisable to make the graft at least 2 to 3 cm long, if possible.

A modification of the bark patch is the bark ring described by Ahlgren (1961). Disadvantages of this method include death of the tree by girdling caused by failure of the bark ring to "take", the greater difficulty in obtaining close contact between edges of the infected and healthy bark tissues, and the need for much more infected material for use in making the rings.

A major consideration in the use of bark-patch grafting is that it bypasses all resistance to initial needle infection and the early stages of establishment. This could be a disadvantage in judging overall resistance of a tree but, on the other hand, might be of help in differentiating needle and bark resistance on an experimental basis. The method has too many disadvantages for use in large-scale testing but it could be useful, for example, in propagating a large number of infections of a single clone in race studies, or in studying the nature of bark resistance.

Needle tissue grafts: Seeking an alternative to foliage inoculation with basidiospores, Boyer (1964) made grafts with infected needle tissue. Small segments of diseased leaves from 0.5 to 5 mm long were inserted into vertical incisions in the stems of young white pine seedlings. Transfer of the fungus was most successful with leaf segments 5 mm long containing the fungus at both ends, while the seedlings were held in a moist chamber for 30 days. Use of this method might prove of value in identification or separation and propagation of different pathogenic races on pine.

The success of all tissue grafting methods seems to depend largely on (1) providing as much opportunity as possible for growth of the fungus from infected to healthy tissues held in close contact, and (2) providing a food base (bark patch or needle segment) large enough to sustain the fungus until it becomes well established in the exposed tissue of the new host.

INOCULUM CONSIDERATIONS

Source of Inoculum

The production of a reasonably homogeneous inoculum is necessary for any large-scale progeny testing program, and for more detailed quantitative studies on the infection process and resistance. Compared with the difficulties and problems encountered by workers who must produce and maintain inoculum of obligate parasites on host plants, growing facultative saprophytes on common laboratory media is a convenience to be jealously regarded by rust workers. But according to Ellingboe (1968), if uniformity of inoculum is a consideration, the natural host-parasite relationship is an advantage, for there seems to be greater uniformity in inoculum produced on the natural host than in inoculum produced on agar media.

Numerous early investigations on blister rust did not come up with any conclusive proof that pine infection from inoculum originating on different ribes species varied in a qualitative manner. Snell (1942) speculated that there was a "threshold" or "quantum" relation between basidiospore production and infection. For artificial inoculation, the concern has been to have as large a production of telia and basidiospores as possible, and this was most easily accomplished by using *Ribes nigrum* L. For many of the inoculations in Wisconsin's Blister Rust Nursery, infected leaves of *R. nigrum* plants still present in some private gardens provided an abundance of inoculum. These had to be supplemented in other years by collections from the native ribes species growing in the wild. The supply of abundant inoculum can be one of the most worrisome problems in large-scale progeny testing programs.

The approach taken by Heimburger in Ontario was to select a strain or strains of *R. nigrum* that retained rust-infected leaves late into the season and to propagate these in a lath house. Rust infection could be initiated by aeciospore inoculations in the spring, if necessary, and uredial intensification provided for an abundance of telial inoculum in the late summer and fall. A similar procedure is being followed for the resistance breeding program conducted by Region 9 of the U. S. Forest Service. Cuttings of Heimburger's leaf-retaining strains were obtained and these are being propagated for establishment of a "rust garden" to serve as an inoculum source for progeny tests.

Storage of Inoculum

The amount of inoculum produced in the wild, or in disease gardens, varies and is subject to the vagaries of the weather. The information that Van Arsdel, Riker, and Patton (1956) presented on the effect of high temperatures, particularly during the telial formation period, on fertility of teliospores possibly helps to explain the occasional poor results experienced in some past inoculations and should be considered in future evaluations of test results. Dependence upon fresh inoculum also makes timing of the actual inoculation subject to weather influences that could affect initial infection and the course of disease development. In the Lake States and southern Ontario where most inoculation tests with eastern white pine have been made, hot dry weather in late summer or early fall has often made it extremely difficult to provide favorable conditions for inoculations, and has probably influenced the viability of the inoculum itself.

The use of fresh inoculum is undoubtedly preferred over stored inoculum, but if large quantities of inoculum could be stored conveniently under conditions that would favor high viability of the teliospores or basidiospores, progeny testing might be greatly facilitated.

Although trials have not been extensive, efforts to store telia for extended periods have not been very successful. Early studies, such as those by Spaulding and Rathbun-Gravatt (1925, 1926), were directed mainly to determining longevity of teliospores or basidiospores in nature. Storage of picked leaves packed in shallow layers between newspapers at about 4°C has been successful for up to a week or so, but we have little information on how long such storage would be successful. If leaves are stored moist, contaminating fungi soon cause deterioration of the leaves and the rust; drying of the leaves and telia, however, can also affect teliospore viability. More remains to be learned about such methods of handling telia-bearing ribes leaves.

The report of successful storage in liquid nitrogen of the telia of *Cronartium fusiforme* Hedgc. and Hunt by Kinloch (1964) and the experience of Loegering, Harmon, and Clark (1966) with liquid nitrogen storage of urediospores of *Puccinia graminis tritici* Erikss. & E. Henn. gave promise that below-freezing storage of telia might be satisfactory. Boyer (1962) found that urediospores, telial columns, and basidiospores all maintained viability for only very short periods when stored frozen at -10°C, alone or over calcium chloride. In a series of trials at Wisconsin (Patton and Johnson)[2] detached telia and telia-bearing ribes leaves were stored under liquid nitrogen with absolutely no success, regardless of prestorage or poststorage treatments.

Greenhouse production of inoculum

Maintaining inoculum in the greenhouse or growth room in smaller quantities for specific experimental purposes also has its hazards, and although these are rarely mentioned in the literature, they are likely to be faced in resistance studies. The extreme susceptibility of ribes to mites requires that close attention be given to preventive and therapeutic sprays with miticides. Changing susceptibility of the leaves and different temperature requirements for production of uredia and telia must be constantly considered. Production of uredia and telia on detached leaves floating on nutrient solutions has been tried, but so far has not proved successful (Boyer, 1962).

INFLUENCING FACTORS

The Components of Inoculation

The emphasis in most inoculation methods is on placing the inoculum at an infection court and providing conditions favorable for reactivation of that inoculum. But since the purpose of inoculation is to obtain infection, further consideration must be given to the fact that each stage of development requires different environmental conditions (Ellingboe, 1968). Germination is but the first step in a series that must occur before infection results, and the events in this series are modified by internal and external factors related to the spore, the host,

[2] *Unpublished data, University of Wisconsin Department of Plant Pathology.*

and the total environment (Bromfield, 1967). I have emphasized in another paper in these proceedings that spore germination and differentiation of infection structures apparently require different conditions. Thus conditions during some latter stage of inoculation may have to vary from those provided in the beginning to reactivate the inoculum. It is here that elements of technique in following a method could be of great importance since the influence of many of the factors may be very subtle indeed.

Effect of Age of Stock

The susceptibility of eastern white pine to infection decreases with increasing age of the stock (Patton, 1961). This influence has been discussed in regard to needle penetrations (Patton, 1967), and resistance (Patton, 1967; Patton and Riker, 1966). In another paper in these proceedings I have mentioned the possible relation of wax plugs in stomata to differences in infection largely between primary and secondary needles, also an age effect. The relation of age to infection seems clear (though the reasons for it may not be), and it seems essential that breeders take it into account in evaluating progeny test results. Patton (1961) pointed out some pros and cons in regard to progeny testing, and Patton and Riker (1966) pointed out specifically in a discussion of the seedbed testing method that, although many factors in progeny testing technique are impossible to control, age of stock is one over which control is possible.

Effect of Fluctuating Temperatures

During the years of work at Wisconsin to develop blister rust resistance in eastern white pine, numerous inoculations have been made, mostly outside and largely successful. In other experiments, inoculations were made in the greenhouse. The criterion for inoculation was to obtain temperatures (and moisture) that were ideal for basidiospore formation and germination; this meant mainly a temperature of about 16°C and not over 20°C. Some infection was obtained under these conditions but usually much less than under outdoor conditions. Moreover, the effectiveness of the inoculation was generally judged on the basis of the percentage of trees that eventually developed cankers, regardless of whether these resulted from a single penetration or from multiple needle infections.

More recently, research was directed toward a study of the infection process and the concern was with needle penetration. It became obvious that, although a constant 16°C temperature was favorable both to casting of basidiospores onto needles and to germination of the basidiospores on the needle surface, infection did not occur at all or so rarely that it was impossible to locate and study the histology of needle penetration.

Finally, experiments on temperature fluctuation were conducted, first in the greenhouse by moving inoculated plants between houses with different temperatures, and later in growth rooms in which the temperature regime was programmed to duplicate as closely as possible representative diurnal temperature fluctuations experienced during successful outdoor inoculations in the Blister Rust Nursery. Outdoor inoculations have been successful with the lower limit at about 4°C and the upper limits ranging from near 16°C to as high, occasionally, as 26°C and even up to 32°C for short periods. Many more or less "standard" runs ranged from about 4°C to 21°C. When the growth chamber was programmed to duplicate this range over a 24-hour period, severe infection was obtained on seedlings ranging in age from 1-1/2 months to more than 5 years.

These results have been confirmed by other studies reported in another paper in these proceedings; differentiation of germ tubes into infection structures--i.e., the vesicle and infection hypha similar to those in the substomatal chamber of a needle at the point of initial infection--occurred to any significant extent only when basidiospores that germinated on collodion membranes were subjected to similar temperature fluctuations. Under such conditions vesicles were found on up to 10% of germinated spores and were typical in shape and size of those formed in needles. Thus, although spore germination occurred readily at a constant 16 or 20°C temperature, the formation of vesicles, which is apparently an essential part of the infection process, was favored by a diurnal temperature fluctuation of about 4.5 to 24°C.

It appears that stimulation of vesicle formation and infection might be the result of a high temperature shock, but further details on temperature limits or timing of fluctuation cycles have not yet been determined. Trials so far have indicated that light has no effect on the differentiation of infection structures, as opposed to the experience of Bromfield (1967) and Emge (1958) with wheat rust. Their results indicated that light plus elevated temperatures had a distinct effect on the later stages of the infection process. Bromfield (1967) made the point, important to consider in relation to white pine blister rust, that cardinal temperatures for infection based on averages or continuous temperatures during dew periods (or in this case, during the inoculation period) fail to permit adequate estimates of the occurrence of infection. Thus the infection process is much more complicated than germination, which is merely the initial step in the sequence.

Some interesting support for this concept is provided by Hirt's (1942) experience with field inoculations of white pine. He found that although pine infection might take place when fluctuating temperatures ranged between about 18°C or below to 21°C or slightly above, temperatures constantly near 20°C or above would inhibit pine infection even though other factors were particularly favorable. Infection occurred usually within a temperature range of 10 to 20°C, but only rarely when temperatures averaged above 21°C. Thus, although a temperature of 20°C or below was necessary for spore germination, some change or fluctuation from this temperature was necessary for initiation of pine infection.

SUMMARY AND CONCLUSIONS

The aim of inoculation techniques is to obtain infection, and several methods have been used with *C. ribicola* on eastern white pine that can fulfill this objective. The major problem, however, is one of standardization; applying a known quantity of inoculum to a known amount of needle surface under conditions favorable to spore germination and initiation of infection so that the end result, either infection or resistance reactions, can be evaluated in a quantitative manner. Most effort so far has made sure that trees will become infected by application of massive doses of inoculum. There has been little or no control of inoculum concentration among trees within a test, or among different tests, and there is little or no information at present on the relation of quantity of inoculum to host response.

Assurance of an adequate supply of inoculum is a prerequisite for progeny testing. For large scale tests, it is almost imperative that a "rust garden" be planted for production of inoculum to be used in artificial

inoculations. Theoretically, exposure of progenies should encompass the broad range of genetic variability in the rust. We still know very little about the existence of pathogenic races of the rust for pine, and if more than one is identified, the problem of how to test progenies against all of these must be faced. This, again, is a problem concerned with source and supply of inoculum.

The major improvement in progeny testing methods and techniques must come from (1) a better understanding of factors influencing needle penetration and initiation of infection, and (2) better ways of applying the basidiospores to the infection court, such as in liquid suspensions, aerosols, or air currents. Ideally, a method is needed that will allow the controlled deposition of inoculum on test plants in a relatively uniform manner, so that disease escape is eliminated and host response can be quantitatively related to inoculum amount. The technique described by Snow (1968) for *C. fusiforme* and modified by Dwinell (these proceedings) is an approach toward this end.

The choice of an inoculation method might depend on whether the objective is large-scale progeny testing or infection for experimental purposes on a relatively small number of individually handled plants. There is need for efficient and reliable methods for both uses, and a successful method designed for small-scale use should be examined with the view of adapting it for large-scale progeny tests of a resistance breeding program.

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FLOOR DISCUSSION

(Discussion here also covers the previous paper by R. T. Bingham.)

MCDONALD: Dr. Patton, your reports on the influence of seedling age on susceptibility have brought a question to my mind. How do you know the effect is not one of genotype? If you are comparing the younger tree of one genotype with the older tree of another it seems to me you can't eliminate this possibility.

PATTON: Although I didn't have time to go into it, I have made tests on the same full-sib progenies at different ages and have obtained the same results. Also, I have inoculated grafts of the same tree at different ages and results have indicated the same sort of age effect. We haven't done much with inoculating a single tree, say at ages 1 and 10 years, but in large-scale progeny tests we found definitely that susceptibility decreases with age.

MCDONALD: Well, I agree with the difference between 1- and 2-year-old seedlings.

PATTON: But we have also observed the same phenomenon with grafts from 4- up to 40- and 50-year-old susceptible trees. In our inoculation tests, as trees from which we collected scions increased in age the number of infections on the scions was reduced considerably. In other words, it was much harder to get infection on a susceptible old tree than it was on a susceptible young tree. I'm not saying that as a tree grows older it cannot become infected; we know that in time a lot of these older trees do become infected.

MCDONALD: As I recall, however, in a table of your 1967, 14th IUFRO Congress Paper[1] you showed only a small difference--of 0.6 substomatal vesicles per cm of needle length in a 4-year-old seedlings and 0.4 in 40-year-old grafts.

PATTON: Yes, I don't consider these differences particularly significant. The main thing demonstrated by this table was the difference in amount of infection we have always obtained between primary and secondary needles.[2] Even though the difference between a secondary needle on a 5-year-old and a 40-year-old tree may not be shown by this table, there does still appear to be some difference in susceptibility of the trees as shown by incidence of stem cankers.

ZUFA: I wish to describe a technique we use at our Research Station in Ontario. We raise test seedlings in 3/4"x3" slit polystyrene tubes, arranged with seedling families replicated and randomized in 200-tube flats. Seed are sown in the greenhouse in January or February and moved, through cold frames, to the outdoors. First-year tubed seedlings are inoculated in late August using inoculation techniques developed by Dr. Heimburger. Shortly after becoming dormant they are moved back into the greenhouse. By the second January (seedling age 12 months) we are able to detect infection with certainty, not only spots on the needles but also of the blister rust mycelium in the seedling stem. Last spring we classified the seedlings according to heavy, medium and light needle infection classes, finding mycelium in all the heavy and medium class seedlings but only in half of the light infection class seedlings. Differences in infection of seedlings in different families were really surprising. The worst family showed 96% heavy and medium infection, the best only 23% heavy and medium infection. We think that on the basis of such a finding we may be able to judge the transmitting ability of trees even in such a short, 12-month-from-seed, period. Later after we moved the 2nd-year seedlings out of the greenhouse, into the nursery, and back into the greenhouse by the next January (24 months after seed germination) aeciospores were produced on the seedlings. I wish to have your comments on these findings. We infected the seedlings while still very young, but they didn't die, at least not all of them. And we found quite surprising differences between the families.

[1] *Editor's note: See Table 1, Patton, R. F. 1967, preceding Literature Cited section.*

[2] *Editor's note: The table being discussed shows 11.0 substomatal vesicles per cm of needle length in 2- to 6-month-old primary needles vs. 0.6 in 4-year-old seedling secondary needles.*

PATTON: As panel leader I note that we're already 10 mintues overtime, so I think it best that we move on to the next paper. However, there will be an opportunity to discuss these inoculation techniques while we're in the Intermountain Station blister rust nursery this afternoon,[3] and also later on. Let's continue with the last paper on this morning's panel.

[3] *Editor's note: Informal nursery discussions later this day brought suggestions that test materials inoculated in the primary-foliage stage might react differently than those inoculated at the 2-year-old, secondary foliage stage--possibly due to anatomical or physiological differences of first- vs. second-year foliages, or to resistance factors differing between the 2 ages of foliage.*

A RAPID TECHNIQUE FOR THE DETERMINATION OF *CRONARTIUM RIBICOLA* MYCELIUM IN WHITE PINE BARK TISSUE

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ABSTRACT

Freshly-collected longitudinal bark sections obtained with a scalpel from living tissue adjacent to suspect *Cronartium ribicola* cankers were killed in 50% ethyl alcohol, stained using a modified safranin-fast green schedule, washed in absolute ethyl alcohol, and mounted in "Euparol" or "Permount." Rust mycelium was detected readily from its bright red-stained nuclei and because of its characteristically wide, green-stained, intercellular hyphae.

INTRODUCTION

Many bark abnormalities, such as shallow and deep lesions, partial girdling and girdling necroses, wound periderm formations, etc., often resemble *Cronartium ribicola* J.C. Fisch. ex Rabenh. symptoms. A technique developed for a rapid and positive confirmation of blister rust mycelium in white pine bark tissue would be of value in such cases.

REVIEW OF LITERATURE

Most microscopic analysis and identification of white pine blister rust has involved embedding or freezing the stem of the host tree and sectioning the material on a microtome (Boyer, 1964, 1967; Waterman, 1955).

Boyer (1967) fixed and embedded his material, then stained with safranin-fast green. Ordinarily this double stain is used in an alcohol series and requires several hours to complete. Waterman's (1955) procedure was shorter. She did not use a fixative and, after boiling the wood block, mounted it on a microtome to obtain sections. Her staining was combined into one step and could be accomplished in 1 hour. Jewell (1958) prepared a rapid stain for rusts using orseillin (or safranin) and aniline blue. He reduced the staining times, but he maintained a multi-stepped staining schedule. The Gram-Jorgensen (1953) staining procedure, used to identify fungi in xylem tissue, requires little time. It takes only a matter of minutes for the stain to take effect.

DESCRIPTION OF TECHNIQUE

Using a smooth, even stroke with a sharp scalpel, cut thin longitudinal sections through to the xylem in the suspect area of the stem of the tree. If a canker is present, take the sample from living tissue in an area adjacent to the canker, not from the canker itself.

Place the freshly collected material in small vials containing 50% ethyl alcohol. Staining fresh material gives the best results. When staining, pour the alcohol from the vial and replace it with the modified Gram-Jorgensen stain. The formula for this stain is as follows:

Fast green	0.5 gm
Safranin	1.5 gm
60% EtOH	200 ml
No filtering	

Place the cap on the vial and shake periodically. After 5 minutes, pour off the stain and replace with 100% ethyl alcohol. Use three 30-second changes of absolute alcohol or continue the changes until no red is removed from the sections. Use Euparol to mount the material directly. With Permount take the material through two changes of xylene.

DISCUSSION

The method of embedding or freezing parts of the stem of the host tree and sectioning the material on a microtome may be satisfactory for cytological studies when large amounts of material cannot be prepared and analyzed immediately. Embedding tissue and using a microtome requires time. This method is not satisfactory if positive confirmation of infection is needed quickly, or if the host tree is a young seedling which cannot be destroyed. In such cases, it is quicker and more advantageous to collect thin slices and to stain, mount and preserve them directly. Permanent slides can be prepared in about 10 minutes using this technique and the modified Gram-Jorgensen staining procedure.

Gram-Jorgensen's staining procedure was modified as follows:

1. The hydrochloric acid was omitted from the original stain. The nuclei were more distinct without the acid even though the hyphal walls were harder to define.

2. Staining was extended from 4 to 5 minutes, as the hyphal walls and particularly the nuclei appeared more visible and clearer.

The lignified cells of the host and all the nuclei stain red. Unlignified cells of the host and the hyphal cells stain a green or greenish-blue. The mycelium can be easily and readily detected by its bright red nuclei, which appear as dots, in comparison to the larger and less distinct nuclei in the cells of the host (Figs. 1 and 2).

The blister rust mycelium can be distinguished from the other fungi as it is intercellular and has very wide hyphae. Hirt (1964) states that the vegetative hyphae are 2.8 to 4.2 μ in diameter and the reproductive hyphae even wider.

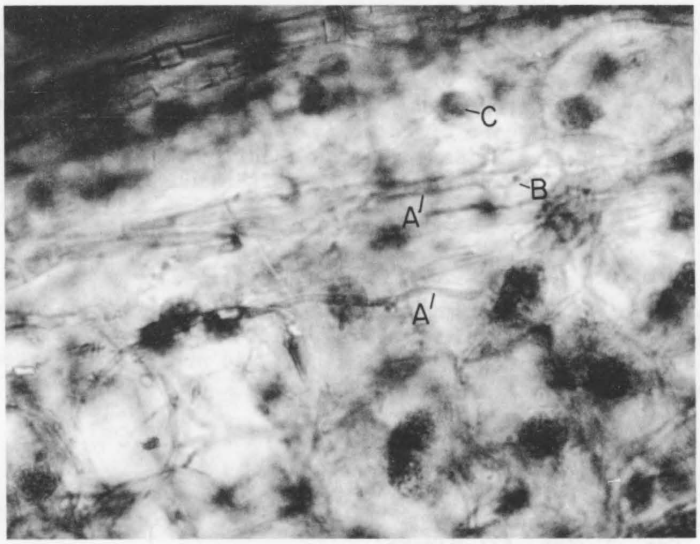


Figure 1. Mycelium of *Cronartium ribicola* in bark tissue of *Pinus strobus* L. (400X): A) hyphal strands of mycelium; B) nucleus of mycelium; C) nucleus of cell of host tissue.

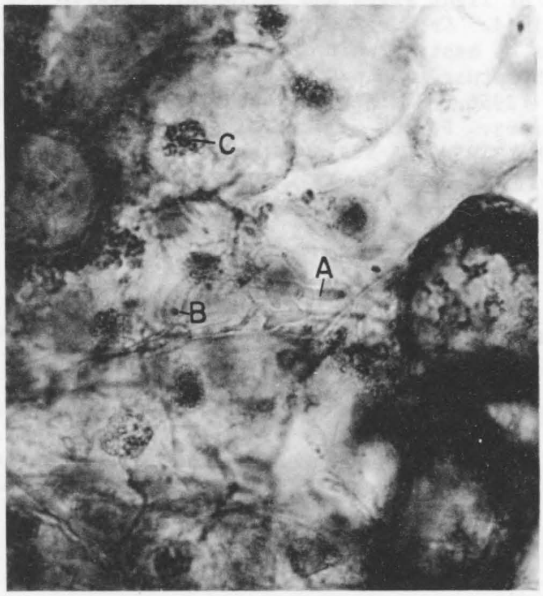


Figure 2. Mycelium of *Cronartium ribicola* in bark tissue of *Pinus strobus* (400 X): A) hyphal strands of mycelium; B) nucleus of mycelium; C) nucleus of cell of host tissue.

The described technique will determine whether blister rust mycelium is present in trees which often lack *Cronartium ribicola* symptoms. It will establish the presence or absence of blister rust in a latent stage in some healthy looking but slow growing, blister rust-inoculated plants. This technique will also be of value for an early confirmation of a blister rust attack, as we were able to identify the blister rust mycelium in the bark tissue of seedlings 5 months after inoculation.

SUMMARY

A double stain consisting of safranin and fast green applied as a single solution gives differentially stained and cleared slides in 10 minutes, showing the wide green hyphae and red nuclei of blister rust when present.

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FLOOR DISCUSSION

SCHÜTT: Can you distinguish blister rust mycelium from mycelium of other organisms, and did you compare blister rust mycelium with mycelium of other organisms?

ZUFA: We did not make any comparison of this kind.

JEWELL: The hastorium shown on the slide identified the fungus as a basidiomycete. Therefore, it's likely that it was blister rust.

TREE RUST INOCULATION PROBLEMS AND TECHNIQUES: SECTION MODERATOR'S SUMMARY

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Inoculations are important in programs of breeding for disease resistance because of the need to test materials. We test to see what we have, or to see if we have what we think we have! Here it is as important to provide a broad base of exposure to the pathogen as it is to provide a broad base for initial selections of the suscept. We don't do this as much in artificial inoculations as we should, perhaps. But natural infection plots situated in various areas help in encompassing a wide range of virulence in strains of the pathogen. Our objective in developing screening methods should be to identify the best selections, the best crosses among these, and the best individuals within these progenies.

Both natural and artificial inoculation methods may be used in screening. With natural inoculations we may have little or no control over the inoculum amount, the environmental conditions, or the time the test may take. Although we should expect natural inoculations to take a long time, to be costly, and often to be unreliable, they nevertheless may have value in aiding interpretation of geographical interactions with climatic or pathogen variation, or of the effects of cultural treatments. Artificial inoculations, on the other hand, can be more efficient and reliable, as was pointed out by Dinus in his comparison between natural and artificial inoculation of slash pine for resistance to fusiform rust.

The source, amount, and availability of inoculum are major considerations in inoculation tests. Collection from wild sources has been depended upon in most tests with *Cronartium ribicola*, *C. fusiforme*, *Melampsora* sp., and *Peridermium pini*. The uncertainty inherent in dependence upon wild sources prompted Heimburger to develop a rust garden as a dependable inoculum source. Artificial inoculation also emphasizes the necessity of being certain about identification of the test organism. For example, Klingstrom had to inoculate peony with aeciospores to screen out unwanted host-alternating strains of *Peridermium pini*. Difficulty in identification of *Melampsora* species complicates the problem of inoculation for resistance to *M. pinitorqua*, and the inability to separate *C. fusiforme* and *C. quercuum* in the telial stage necessitates production of inoculum from a known source.

Inoculum viability is sometimes assumed when it really should be checked. Telia-formation temperature has a pronounced effect on the fertility of telia of *C. ribicola*. Klingstrom noted that although telia of *M. pinitorqua* overwinter on aspen leaves, maturation does not occur until spring and premature collection of inoculum must be avoided. Good storage techniques for inoculum of known viability would be a help in

standardizing inoculations. Successful storage is relatively easy and is feasible for some pathogens, such as *Melampsora* on aspen leaves, or the aeciospores of *P. pini*, but a good storage method for telia of *Cronartium* species would be very helpful.

Successful inoculation presumes a certain amount of knowledge of the infection process. The basic objective must be kept in mind. Screening methods that bypass critical steps in the infection process or in resistance reactions may be all right as long as we are aware, but inoculation results may be misinterpreted if such bypassing is ignored or unintentionally overlooked. It appears that one hindrance to a successful inoculation technique for *P. pini* may be lack of information about the infection process.

We have heard about several major types of inoculations with tree rust fungi. The basic method for large-scale inoculations with *C. ribicola*, *C. fusiforme*, and *M. pinitorqua* is to induce *casts of basidiospores* from teliospores directly onto test material. This has been a simple and efficient method, but no standardization or quantitative evaluations have been possible. Monitored spore casts in an air stream in chambers as described by Snow and by Dwinell are attempts at standardization for laboratory trials. Perhaps a modification of the method could be adapted for large-scale progeny testing. *Dusting dry spores* onto plant surfaces is a commonly used technique with aeciospores or urediospores of *Cronartium* rusts on the alternate hosts, but was not very successful in inoculation of pine with aeciospores of *P. pini*. *Spore suspensions* have been used largely for experimental inoculations. Spray applications of spore suspensions are appealing but have given little success so far, whereas their injection into tissues by hypodermic syringe has proved useful as an experimental technique with *P. pini* and *C. fusiforme* but is hardly adaptable to a large-scale progeny screening method. *Tissue grafts* both with infected needle tissue and bark tissue may prove most useful in experiments on the differentiation of resistance or on races of rust. At present the lack of standardization of inoculum for a natural type of infection is one of the greatest gaps in screening in rust-resistance programs.

Many factors will influence the outcome of our inoculations and the interpretations to be made from them. Host age effects have been noted with *C. ribicola* and *P. pini*. Host vigor may be of particular importance in making comparisons of progeny or selection tests in different areas. The rigor of the test, as exemplified by inoculum amount, has always been a point of controversy. Most workers believe it is safer to err on the conservative side by screening large numbers of plants with heavy spore dosages, even at the risk of losing some valuable materials, rather than to err on the other side by screening too lightly.

In conclusion, it seems that although we do have some relatively successful inoculation techniques, if infection is a measure of success, still we have no reason to be smug about our progress. Our methods so far are not very sophisticated and often result in more problems than efficiency. We are still handicapped by many gaps in our knowledge of the basic infection biology of probably all the rusts in which we are interested. In particular, we need means for standardizing amounts of inoculum applied and for quantifying the host responses, including good indices of infection and resistance reactions.

COMPUTERIZED MAPPING OF BLISTER RUST EPIDEMICS IN NURSERY SEED BEDS

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ABSTRACT

As part of a long-range U.S.D.A. Forest Service program for development of varieties of *Pinus monticola* resistant to *Cronartium ribicola*, 2-year-old seedling progenies were artificially inoculated in nursery seed beds. Success of inoculation varied, especially across long seed beds or several seed beds that had been inoculated simultaneously. Because of the variation, rejection of lightly or non-inoculated portions of seed beds was essential to the validity of analyses. Because of this problem and the large body of test data involved, a FORTRAN IV computer program was designed to process data and produce maps showing blister rust needle-lesion frequency on individual seedlings within nursery beds.

In the fall of 1964, seeds were planted in an Intermountain Forest and Range Experiment Station nursery at Moscow, Idaho, to test more than 100 parents for transmission and heritability of blister rust resistance in western white pine. The seeds were sown in 5,790 rows and all seed spots (16 per row) identified. This planting produced 61,000 seedlings.

All seedlings were artificially inoculated with *Cronartium ribicola* at age 2. About 10-12 months later, all were examined for needle-lesion frequency. Success of inoculation varied; especially across long seed beds or across several seed beds that had been inoculated simultaneously. To detect inoculation "cold spots" a computer program was written that would produce maps of the seed beds showing the intensity class of needle-lesion frequency for each seedling. Mapping enabled us to delete from further analysis data from lightly or noninoculated portions of seed beds.

A 13-row portion of a seedling bed is shown on the sample map (Fig. 1). Row number and parent identification are to the left of each row. The seeds were sown in two subrows (eight seed spots per subrow). Blank spaces in a row indicate that no seedlings are growing in those seed spots; double letters indicate that two seedlings are growing in a seed spot. The area delineated by the broken line contains seedlings with no needle lesions. Since this "cold spot", or noninoculated area, runs across several rows, including a control (9995 x 999), the seedlings within this area were rejected from further analysis.

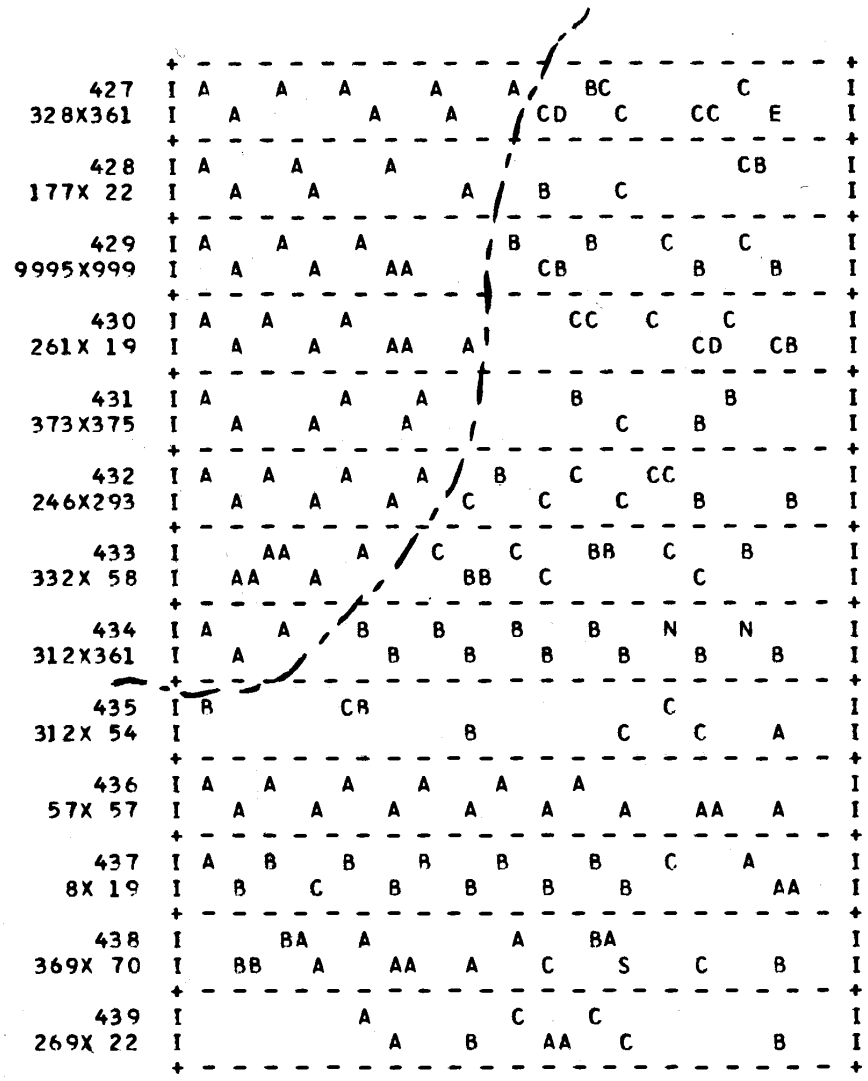


Figure 1. An example of a needle-lesion frequency map of a seedling bed produced by computer: A = no lesions; B = 1-5 lesions; C = 6-25 lesions; D = 26-100 lesions; E = 100+ lesions; N = foliage non-readable (dead, dying, or missing) at time of examination; S = no lesions at time of examination; but canker later developed. Note the resistant progeny 57 x self.

The mapping program was designed specifically to map rust intensity in progenies tested according to standardized tests in use here. Because it is applicable only to the design in use here, the program is not available for distribution. However, information pertaining to the methodology of mapping to the acquisition and reduction of test data will be provided by the author upon request.

ESTIMATION OF HERITABILITY AND SELECTION GAIN FOR BLISTER RUST RESISTANCE IN WESTERN WHITE PINE

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ABSTRACT

Disease-free western white pines (*Pinus monticola*) were located in northern Idaho and crossed with four tester trees. Seed progenies from crosses were sown in the fall of 1964 at the Intermountain Forest and Range Experiment Station's nursery in Moscow, Idaho, and seedlings therefrom were exposed to the blister rust disease pathogen (*Cronartium ribicola*) in the fall of 1966 during the seedlings' second year of growth. Two years later (fall, 1968) the proportion of healthy seedlings per plot was determined and the plot data adjusted for small numbers and transformed to the arc sine of the square root of the proportion (the derivation of the binomial model and transformation is explained in an appendix).

In a factorial analysis of variance estimates of additive genetic and dominance variance were obtained. Dominance variance was high in relation to additive variance. Heritabilities for selection on an individual basis for three elevation groups were: 5, 3.2%, and 7.0%. Heritabilities for selection by progeny testing candidate trees ranged from 38.6% to 66.0%. The predicted selection gains were: selection of candidate trees in the forest, 11.3 to 23.1%; selection of candidate trees by progeny testing, 3.5 to 8.4%; selection of individual seedlings based upon ability to remain healthy after artificial inoculation, 0.1 to 1.4%. The total gain ranged from 14.9 to 30.5%.

The heritabilities and selection gains from the last two methods were lower than had been previously reported from this experiment station. Gains for the selection of healthy trees in the forest were greater than previously obtained possibly due to the inoculation of the seedlings during their second growing period than during their first growing year.

Disease-free mature western white pine (*Pinus monticola* Dougl.) trees located in heavily infected areas (candidates) from three elevations (low - below 3,299 feet; mid - 3,300 to 4,099 feet; high - 4,100 feet and above) were crossed with tester trees from their own elevational zone. In fall,

1964 the seed from these crosses were sown in a randomized block design in the nursery at the Intermountain Forest and Range Experiment Station, Moscow, Idaho. Concurrently, along with the pedigree matings, control seeds collected from 10 random sources were planted in the nursery. The conditions followed were the same as those reported for the 1960, 1962, and 1963 progeny tests (Bingham *et al.*, 1969) except that the seedlings were exposed to white pine blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) during their second seedling year rather than during their first seedling year.

The seedlings were examined 1 and 2 years after exposure to the blister rust disease pathogen (*Cronartium ribicola*).

There were three stages to which selection could have been carried out in this breeding program, each stage culminating in progressively better seed orchards (Fig. 1). For stage A, the blister-rust-free candidate trees could have been selected from among dead and diseased trees in heavily rusted natural stands in the forest, and seed orchard "A" established by grafting from all selected trees. The second stage (B) could have been attained by progeny testing of the candidates and establishing seed orchards by grafting only from those trees selected for general combining ability (i.e., having all 4 test-cross progenies exhibiting above-average survival levels). The third stage (C) could have been attained by exposing the progeny of the stage B matings to the disease pathogen, selecting those seedlings that survived exposure, and mating them in a seedling seed orchard.

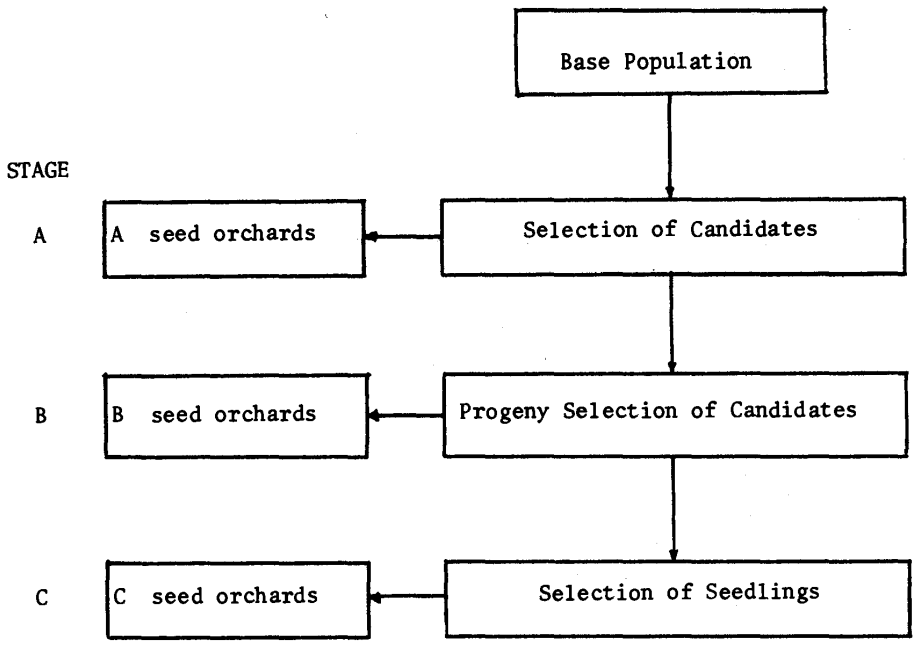


Figure 1. Alternative breeding and seed orchard establishment schemes.

The models from which estimates of genetic parameters were obtained to predict selection gains in stages B and C follow.

MODELS

STATISTICAL

Each elevation was analyzed separately and the general formula for the statistical model was:

$$X_{ijk} = \mu + \tau_i + \chi_j + (\tau\chi)_{ij} + R_k + b_{ijk} + e_{ijk} + d_{ijk}$$

X_{ijk} = adjusted and transformed proportion of healthy seedlings, from the cross of the ith tester and the jth candidate, in the kth replication; μ = general mean; τ_i = effect of ith tester; χ_j = effect of jth candidate; $(\tau\chi)_{ij}$ = effect of interaction of the ith tester and the jth candidate; R_k = effect of the kth replication; b_{ijk} = binomial sampling effect; e_{ijk} = effect of plot; d_{ijk} = individual effects within a plot.

The candidates and testers were considered to be random with the replications fixed.

The basic data of the experiments consisted of the proportions, number healthy seedlings (n_{ijk}) divided by the total number (m_{ijk}) per plot.

$$P_{ijk} = \frac{n_{ijk}}{m_{ijk}}$$

An adjustment was made to the proportion (Bartlett, 1947) to minimize fluctuations, due to small sample sizes, as follows.

When $n_{ijk} = m_{ijk}$

$$P_{ijk} = 1 - \frac{1}{4\, m_{ijk}} \quad ,$$

and when $n_{ijk} = 0$

$$P_{ijk} = \frac{1}{4\, m_{ijk}} \quad .$$

The adjusted proportions were transformed to arc sin of square root of the proportion (Bartlett, 1936) to stabilize the variance. The variance of the proportions was

$$\sigma^2_P = \frac{1}{\overline{m}}\ P(1\text{-}P) - \frac{1}{\overline{m}}\,\sigma^2_d$$

where $P(1\text{-}P) = \sigma^2_b$ and is the binomial sampling variance, σ^2_d is the variance of the inequality of the probabilities of each seedling being healthy (see Kendall and Stuart, 1963, p. 127 and Appendix to this paper) and $\overline{m}$ is the harmonic mean of the number of seedlings per plot. With the adjusted proportions transformed to arc sin the binomial sampling variance is constant (Scheffé, H., 1959) and equal to 821 (Fisher and Yates, 1948, and see Appendix for explanation) and therefore

$$\sigma^2_P = \frac{1}{\overline{m}} 821 - \frac{1}{\overline{m}} \sigma^2 d \,.$$

Table 1 gives the analysis of variance model with the expectations of mean squares assuming candidates and testers random and replications fixed. The variances $\sigma^2 e$ and $\sigma^2 d$ cannot be separated and therefore $\sigma^2 e - \frac{1}{\overline{m}} \sigma^2 d$ is one term.

GENETIC

Table 2 gives the genetic meaning in terms of covariance of relatives of the variance components of table 1 as well as the designation of binomial sampling and environmental variances.

Estimation of Heritabilities and Prediction of Selection Gain

Heritabilities were obtained by considering them as regression coefficients of future progeny on the test material. The general formula would be

$$h^2 = \frac{\text{covariance (test material--future progeny)}}{\text{variance of selection units}}$$

where the test material are the measured individuals and selection units are the units used for selection such as individuals, means of full or half sib families, or means of progeny. For selection on an individual basis (stage C in Fig. 1) the selection gain would be

$$\Delta G_{♀♀} = S_D \frac{\text{cov (dam-daughter)}}{\sigma^2_{P(D)}} + S_S \frac{\text{cov (sire-daughter)}}{\sigma^2_{P(S)}}$$

$$\Delta G_{♂♂} = S_D \frac{\text{cov (dam-son)}}{\sigma^2_{P(D)}} + S_S \frac{\text{cov (sire-son)}}{\sigma^2_{P(D)}} \,,$$

where the sexes are kept separate both in the progeny, daughters (♀♀) and sons (♂♂), and in the parents. The dams (D) are the maternal parents and the sires (S) are the paternal parents, with P = phenotype; S = selectional differential; and ΔG = selection gain. The covariances of parent-offspring each estimates 1/2 additive genetic variance. However, because pine trees are monoecious the terms and separate equations for daughters and sons must be combined, and

$$\Delta G = S \frac{2 \text{ cov (parent-offspring)}}{\sigma^2_P} \,.$$

In the design used in these experiments the covariance of parent offspring was not measured. Twice the covariance of candidates half sibs ($2 \sigma^2_C$) was substituted for cov (parent-offspring), giving

$$\Delta G = S \frac{4 \sigma^2_C}{\sigma^2_T + \sigma^2_C + \sigma^2_{TC} + \frac{1}{\overline{m}} \sigma^2_b + (\sigma^2_e - \frac{1}{\overline{m}} \sigma^2 d)} \,,$$

with $\overline{m} = 1$ because individual selection was practiced.

Table 1. Model for analysis of variance (testers and candidates assumed random; fixed replications)

Source of variation	d.f.[a]	Mean squares	Expectation of mean squares[b]
Replications	K-1	MS_R	
Testers	I-1	MS_T	$\sigma^2_e + \frac{1}{\overline{m}}\sigma^2_b - \frac{1}{\overline{m}}\sigma^2_d + K\sigma^2_{TC} + KJ\sigma^2_T$
Candidates	J-1	MS_C	$\sigma^2_e + \frac{1}{\overline{m}}\sigma^2_b - \frac{1}{\overline{m}}\sigma^2_d + K\sigma^2_{TC} + KI\sigma^2_C$
Tester X Candidate	$(I-1)(J-1)$	MS_{TC}	$\sigma^2_e + \frac{1}{\overline{m}}\sigma^2_b - \frac{1}{\overline{m}}\sigma^2_d + K\sigma^2_{TC}$
Tester-Candidate combinations X Replications	$(IJ-1)(K-1)$	MS_{TCR}	$\sigma^2_e + \frac{1}{\overline{m}}\sigma^2_b - \frac{1}{\overline{m}}\sigma^2_d$

[a] I, J, and K = total numbers of testers, candidates, and replications, respectively.

[b] Formulas for estimating individual variance components are as follows:

$$\sigma^2_T = \frac{MS_T - MS_{TC}}{KJ}$$

σ^2_T = variance due to testers

$$\sigma^2_C = \frac{MS_C - MS_{TC}}{KI}$$

σ^2_C = variance due to candidates

$$\sigma^2_{TC} = \frac{MS_{TC} - MS_{TCR}}{K}$$

σ^2_{TC} = variance due to interaction of testers and candidates

$$\sigma^2_e - \frac{1}{\overline{m}}\sigma^2_d = MS_{TCR} - \frac{1}{\overline{m}}\sigma^2_b$$

σ^2_e = variance due to effect of plot

σ^2_d = variance due to effect of individuals

σ^2_b = 821

σ^2_b = variance due to effect of binomial sampling

$$\overline{m} = \frac{IJK}{\Sigma \frac{1}{m_{ijk}}}$$

$\overline{m}$ = harmonic mean number of seedlings

Table 2. Genetic and environmental model of covariances of relatives

Variance component[a]	Proportion of variance contributed by each source					
	Genetic variance			Environmental variance		
	Additive	Dominance	Epistatic	Between plots	Within plots	Binomial variance
σ^2_T	1/4	0	>1/16	0	0	0
σ^2_C	1/4	0	>1/16	0	0	0
σ^2_{TC}	0	1/4	>1/8	0	0	0
σ^2_e	0	0	0	1	0	0
σ^2_b	0	0	0	0	0	1
σ^2_d	1/2	3/4	<3/4	0	1	0

[a] $\sigma^2_T = \text{cov}_{S(T)}$ (covariance tester half sibs)
$\sigma^2_C = \text{cov}_{S(C)}$ (covariance candidate half sibs)
$\sigma^2_{TC} = \text{cov}_f - \text{cov}_{S(T)} - \text{cov}_{S(C)}$ (cov_f = covariance full sibs)
σ^2_e = environmental variance between plots
σ^2_b = binomial sampling variance
$\sigma^2_d = (\sigma^2_G - \text{cov}_f) + \sigma^2_W$ (σ^2_G = total genetic variance; σ^2_W = environmental variance within a plot

The term $(\sigma^2_e - \frac{1}{\bar{m}} \sigma^2_d)$ can be estimated accurately only when $\bar{m}$ is equal to the actual harmonic mean. For $\bar{m} = 1$, this term is overestimated and, therefore the gain is underestimated depending upon the magnitude of σ^2_d.

If the actual selection differential is not known but the proportion selected is, then $S = i\ \sigma_P$ where i can be obtained from tables (e.g., Becker, 1967) for a given percent selected and σ_P is the phenotypic standard deviation.

Heritability where candidate trees were selected for general combining ability on the basis of their progeny means and these candidates remated together (stage B) was also estimated. The future progeny of a candidate and the candidate's tested offspring were half sibs because they had one parent in common (the candidate) and, therefore, the numerator was the covariance of half sibs. The denominator was the variance of the selection units which in this case were the means of the candidate's progenies. The selection gain was:

$$\Delta G = S_D \frac{\sigma^2_C = \text{cov}_{S(C)} \text{ (candidate half sibs)}}{\sigma^2_C + \sigma^2_T/I + \sigma^2_{TC}/I + \sigma^2_{TCR}/K} + S_S \frac{\sigma^2_C = \text{cov}_{S(C)} \text{ (candidate half sibs)}}{\sigma^2_C + \sigma^2_T/I + \sigma^2_{TC}/I + \sigma^2_{TCR}/K},$$

where

$$\sigma^2_{TCR} = \sigma^2_e + \frac{1}{\bar{m}}\sigma^2_b - \frac{1}{\bar{m}}\sigma^2_d$$

But, because pine trees are monoecious the terms combine and

$$\Delta G = S \frac{2\,\sigma^2_C}{\sigma^2_C + \sigma^2_T/I + \sigma^2_{TC}/I + \sigma^2_{TCR}/K}$$

RESULTS

Because of the large number of individual seedlings involved in each test, the statistical analyses of stage B were done on an electronic computer. A special set of computer programs was written to edit the data, compute the statistical analysis, and produce maps (printer plots) of infection locality and intensity (for these maps see McCluskey, these proceedings).

Progenies from the three elevation zones were analyzed separately. Included in the program output were: an analysis of variance table; a table of variance components; and a table of the percent healthy seedlings for each of the tester-candidate combinations. This last table was sorted on the average percent healthy for each candidate over all testers.

The degrees of freedom (df) and mean squares (MS) of the analysis of variance of adjusted and transformed data are given in Table 3. The variance components and their standard errors are given in Table 4. The harmonic mean number of seedlings ($\bar{m}$) for each elevation was: 8.39 low, 8.26 mid, and 6.26 high. These seedlings had been exposed to blister rust during the fall of their second growing season and, as expected, the means of healthy seedlings were higher (56.67%, 44.86%, and 54.23%) than had previously been reported (Bingham *et al.*, 1969) for seedlings exposed to the pathogen during their first growing season.

The estimates of 1/4 additive genetic variance provided by σ^2_T and σ^2_C ranged from 3.48 to 18.28. The interaction variance σ^2_{TC} which estimates 1/4 dominance variance and about 1/8 of epistatic variance was high in relation to the estimates of additive genetic variance in each elevational zone.

The heritabilities were calculated for individual and progeny tests for each elevation in accordance with the procedures given previously. Table 5 presents these heritabilities by elevational zones and method of selection.

To illustrate the calculations required for estimating heritability the mid elevational zone data are taken from Table 4.

Table 3. Analysis of variance of adjusted and transformed data

Source of variation	Elevation					
	Low		Mid		High	
	d.f.	MS	d.f.	MS	d.f.	MS
Replications	9	12,694	9	11,237	9	4,209
Testers	3	2,134	3	2,433	3	3,023
Candidates	50	877	20	714	16	1,144
Tester X Candidate	150	361	60	374	48	413
Tester-Candidate combinations X Replications	1,827	276	747	316	603	305

Table 4. Means of healthy seedlings and variance components

Component[a]	Elevation		
	Low	Mid	High
Mean (%) candidates	56.67	44.86	54.23
controls 33.56			
σ^2_T	3.48 ± 2.65	9.81 ± 7.33	15.36 ± 11.26
σ^2_C	12.90 ± 4.40	8.50 ± 5.64	18.28 ± 9.75
σ^2_{TC}	8.43 ± 4.24	5.75 ± 6.91	10.73 ± 9.59
$\sigma^2_e - \frac{1}{m}\sigma^2_d$	178.57	217.07	174.32
$\frac{1}{m}\sigma^2_b$	97.80	99.43	131.16

[a] Standard error of variance components were obtained according to Anderson and Bancroft (1952).

Table 5. Heritabilities (%) for different selection methods and elevational zones, when selecting for healthy seedlings

Selection method	Elevation		
	Low	Mid	High
Individual	5.0	3.2	7.0
Progeny test (= selection unit)	59.3	38.6	66.0

1. Heritability when individuals are selected on the basis of their being healthy after exposure to the pathogen (stage C), $\bar{m} = 1$, is

$$h^2 = \frac{4\,\sigma^2_C}{\sigma^2_T + \sigma^2_C + \sigma^2_{TC} + \frac{1}{\bar{m}}\sigma^2_b + (\sigma^2_e - \frac{1}{\bar{m}}\sigma^2_d)} ,$$

$$= \frac{4(8.50)}{9.81 + 8.50 + 5.75 + 821 + 217.07} ,$$

$$= \frac{34.00}{1062.13} = 0.032 .$$

2. Heritability when candidates are selected for general combining ability on basis of their progeny performance and selected candidates are mated together (stage B) is

$$h^2 = \frac{2\,\sigma^2_C}{\sigma^2_C + \sigma^2_T/I + \sigma^2_{TC}/I + \sigma^2_{TCR}/K} ,$$

and again using the mid elevational zone data as an example:

$$= \frac{2\,(8.50)}{8.50 + 9.81/4 + 5.75/4 + 316/10} ,$$

$$= \frac{17.00}{43.98} = 0.386 .$$

These heritabilities were used to determine the selection gains for stages B and C (Table 6). The gain for stage A was obtained by subtracting the mean of the controls (33.56%) from the mean of the crosses for the particular elevation.

Table 6. Predicted selection gains, in percent, by stages and elevations

Stage	Selection basis	Elevation		
		Low	Mid	High
A	Natural selection in forest	23.1	11.3	20.7
B	Progeny tests of candidates	5.4	3.5	8.4
C	Individuals artificially inoculated	0.1	0.1	1.4
A+B+C		28.6	14.9	30.5

The gains for stage A were much larger than given previously for the 1960, 1962, and 1963 progeny tests (Bingham *et al.*, 1969). Within an elevational zone stage A gains were larger than either stage B or C gains.

The total gains for all three methods of selection varied from 14.9% to 30.5%.

DISCUSSION

The results from the quantitative genetic analysis showed that the gains from selection for healthy trees in the forest (stage A) were greater than previously reported. This difference is probably due to the fact that inoculation of seedlings in the 1964 test occurred during the second rather than during the first growing season.

Also the heritabilities were in general lower for the selection unit method of selection than had been estimated previously. One factor affecting the heritability was the high estimate of dominance and epistatic variance as compared with the estimate of the additive genetic variance in each elevational zone. The high estimate of dominance and epistatic variance could be a result of a few dominant major genes for resistance or susceptibility segregating in the population.[1]

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[1] *Editor's note: The reader is directed to Hoff and McDonald's paper in these proceedings, where dominance (single major gene effects controlling resistance) is brought out.*

APPENDIX

DERIVATION OF BINOMIAL MODEL AND TRANSFORMATION

BINOMIAL MODEL

Each seedling within a plot is a sample from a population. The populations differ from each other in their probability of a seedling being healthy because of genetic segregation (seedlings are full sibs to one another) and because of environmental effects (seedlings are planted in different spots within the plot). The basic datum is the proportion of healthy seedlings divided by the total number of seedlings per plot. Because each seedling has a different probability of being healthy the standard binomial model does not apply.

If we can use the number of healthy seedlings per plot as an observation (n_{ijk}), then the variance of this observation is

$$\sigma^2_n = \sum_{h=1}^{m} p_h q_h \ ,$$

where p_h is the probability of the hth seedling being healthy and q_h is $1 - p_h$, $h = 1,2,\ldots m$ within a plot.

$$\sum_{h=1}^{m} p_h q_h = \sum_{h=1}^{m} p_h (1 - p_h) = \sum_{h=1}^{m} p_h - \sum_{h=1}^{m} p^2_h \ ,$$

$$= \sum_{h=1}^{m} p_h - \frac{1}{m} \left(\sum_{h=1}^{m} p^2_h \right) - \left[\sum_{h=1}^{m} p^2_h - \frac{1}{m} \left(\sum_{h=1}^{m} p_h \right)^2 \right]$$

$$= m \bar{p} - m \bar{p}^2 - m \sigma^2_d \ ;$$

where $\bar{p}$ is the mean of the p's in the different populations; σ^2_d is the variance due to the populations within a plot being different; and m is the total number of seedlings per plot.

$$\sum_{h=1}^{m} p_h q_h = m \bar{p} \bar{q} - m \sigma^2_d \ .$$

$\bar{P}_{ijk}$ is the proportion of healthy seedlings in a plot (ith tester, jth candidate, and kth replication) and is calculated by

$$\frac{n_{ijk}}{m_{ijk}} \ .$$

The variance of $\bar{p}$ for a plot is the variance of the number of healthy seedlings per plot divided by the square of the total number of individuals (m^2)

$$\frac{1}{m^2} \sum_{h=1}^{m} p_h q_h \ .$$

Therefore

$$\sigma^2_p = \frac{1}{m}\bar{p}\,\bar{q} - \frac{1}{m}\sigma^2_d$$

where $\frac{1}{m}\,\bar{p}\,\bar{q}$ is the binomial sampling variance.

The variance of the proportion therefore is less than the standard binomial variance by $\frac{1}{m}\sigma^2_d$.

ARC SINE SQUARE ROOT TRANSFORMATION

If $\bar{p}$ is the average probability of a seedling within a plot being healthy then the number of healthy seedlings is $n = m\,\bar{p}$, the expected value of n, $E(n) = \mu$.

The binomial sampling variance $m\,\bar{p}\,(1 - \bar{p})$ is a function only of the mean probability of a seedling being healthy, μ. The standard deviation (σ_μ) is a function of μ,

$$\sigma_\mu = \phi(\mu) = [\mu(1 - m^{-1}\mu)]^{1/2}\ .$$

We can remove this dependence of the variance on the mean if we can find a function of the mean $f(\mu) = Z$, such that the new variable Z has a constant variance (Scheffé, 1959, p. 365). Let the standard deviation of Z be equal to the standard deviation of μ, times the derivative of the function $f(\mu)$,

$$\sigma_Z = \sigma_\mu\ f'(\mu),$$

Then

$$f'(\mu) = \sigma_Z/\sigma_\mu = \sigma_Z\ /\ \phi(\mu).$$

The function $f(\mu)$ which gives a new variable Z, constant variance can be obtained by the integration of $f'(\mu)$,

$$f(\mu) = \int f'(\mu)\ du = \sigma_Z \int \phi(\mu)^{-1}\ du.$$

Substituting the estimate $\bar{p}$ for $m^{-1}\mu$ will give

$$f\ (\bar{p}) = \sigma_Z \int m\,\bar{p}\ \ (1 - \bar{p})\ d\,\bar{p}\ ,$$

$$= 2\ m^{1/2}\ \sigma_Z\ \arcsin\ (\bar{p})^{1/2} + c$$

The above function can be simplified by taking $c = 0$, and choosing $\sigma_Z = 28.65\ m^{1/2}$.

$$f\ (\bar{p})\ -\ \arcsin\ (\bar{p})^{1/2}$$

for the arcsin in degrees.

Therefore the variance of the transformed proportion of healthy seedlings within a plot is

$$\frac{1}{m} 821 - \frac{1}{m} \sigma^2_d .$$

The first term is the binomial sampling variance, the second term is the variance due to individual seedlings within a plot differing from the mean plot value ($\bar{p}$).

PANEL IV

PATHOLOGY AND GENETICS OF TREE RUST RESISTANCE
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MELAMPSORA PINITORQUA (BRAUN) ROSTR. AND *PERIDERMIUM PINI* (WILLD.) KLEB. ON PINES - SOME ASPECTS

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ABSTRACT

Pine terminal shoots normally contain several substances that have an inhibiting effect on *Melampsora* basidiospore germination. The amount of inhibitors declines in conjunction with the axial extension of the pine, about the time when infection by *Melampsora pinitorqua* occurs. Germination-inhibiting substances have also been found in leachates from the surface of pine shoots. Clones and progenies of *Pinus silvestris* with different attack frequencies as regards *Melampsora pinitorqua* have been described. Clones with different degrees of sensitivity to the disease can also differ as regards the inhibitor content. The difficulty of registering the attack frequency in an acceptable way has also been dealt with.

As regards *Peridermium pini*, an account is given of an inoculation test on progenies produced for studying the fungus in question.

Studies of these endemic rusts on pines, aimed at practical breeding in Sweden, are still at an early stage. No drastic event, such as the introduction of white pine blister rust into the North American continent, has to similar degree focused interest and resources on these parasites.

MELAMPSORA PINITORQUA

A number of European pine species are susceptible to attack by *Melampsora pinitorqua* (Braun) Rostr. Several American pine species used in European tests also have shown themselves to be susceptible. An attempt to summarize the results of these tests has recently been made by the author (Klingström, 1969).

INFECTION BIOLOGY

The actual infection biology is still not fully known. Basidiospores usually are not disseminated over large areas; the danger zone is generally considered to be about 200 meters. A summary of available reports on spread of this rust has been made by Regler (1957). The usual

point of attack is the annual shoot. Needles on seedlings 2-4 weeks old (Regler, 1957) or older (Klingström, 1963) can carry aecidia. In the latter case the rust establishes itself on the needle tip. Younger pines are damaged more noticeably by the fungus. As the pines increase in age, injuries of a fatal nature decrease, but the number of injuries which lead to deformation increase (Böhner, 1952; Regler, 1957). Under Swedish conditions, older pines can also be attacked (Kardell, 1966).

The germination of basidiospores has been studied in laboratory tests (Klingström, 1963, 1969) and has also been used for bioassay in studies of, among other things, inhibitors in *Pinus silvestris* L. (Klingström, 1969). However, a detailed study of infection biology in the field remains to be made. Usually pycnia develop before a caeoma with aeciospores is formed, but the function of the pycnia is unclear. There is, however, reason to make comparisons with tests on other species of *Melampsora*, in which exchange of pycnial fluid is necessary (Ziller, 1965).

The establishment of the fungus on pine usually takes place during periods when a fortuitous coincidence of suitable weather for the formation and distribution of basidiospores occurs with the axial extension of succulent pine shoots. Substances with an inhibitory effect on basidiospore germination can be traced to the surface of pine shoots, e.g. to leachates in drops of water. Other substances in the pine shoots which have a similar inhibiting effect on spore germination undergo a considerable decline in conjunction with axial extention (Klingström, 1969). Experiments have included both studies of *Melampsora* basidiospore germination and *Avena* straight growth test. In general these have given similar results.

RESISTANCE BIOLOGY

Weather conditions, biologically active surface deposits, possibly in conjunction with leaching, and a decline in the amount of inhibitors in pine shoots during axial extension are possible factors influencing the natural occurrence of *M. pinitorqua*. There have also been individual reports about differences in the frequency of *Melampsora* in different pine material. Rennerfelt (1954), Bergman (1954), and Klingström (1963, 1969) have examined the differences in the attack frequency between different plus tree clones. Eklundh Ehrenberg (1963), Schütt (1964, 1965), Hattemer (1965), Illy (1966), and Klingström (1969) have presented results concerning differences in the attack frequency between progenies. Certain germ plasm useful for resistance breeding seems to be available, although there is as yet no breeding work using such resistant pine material. But it is too early to discuss inheritance, genes involved, heritability, combining ability and so on. The works cited indicate that differences in attack frequency exist between clones and between progenies and, further, that general combining ability may hold with certain parents. It should be possible to put these results to practical use in pine seed orchards with suitable clones. However, further tests are necessary.

Even though pine materials of particular interest in the study of *Melampsora* should become available, the question of how to score attack by the twist rust in an acceptable way is still to be solved. This is particularly the case with pines 3 years or more of age. Scoring number of lesions per pine does not take into consideration host variation in size or the number of first whorl shoots. Neither does number of lesions per shoot take size into consideration, but classes terminal leaders and

first whorls equally. Scoring the percentage of healthy - or diseased - pines per progeny fails to separate pines with isolated attacks from pines that may have sustained very serious attacks. From the practical aspect it would be more useful to know the percentage of pines with permanent damage caused by *Melampsora* during, say, a 5-year period. The attack frequency is higher for terminal leaders than for first whorls, and damage to terminal leaders is of course of greater practical interest. Thus attacks per cm of terminal leader is a reasonable scoring method for *M. pinitorqua* on somewhat older pines.

When making routine progeny tests one consideration is whether exposure to *Melampsora* should be limited to the pines' second year in nurseries, or in plastic greenhouses under controlled conditions, *Pinus silvestris* L. has no branches at this stage and *Melampsora* damage on the pine stems is frequently serious. At this stage the percentage of infected plants per progeny is an acceptable way of scoring *M. pinitorqua* attack.

Sometimes, however, the number of attacks per progeny is not necessarily in proportion to permanent damage. One investigation (Klingström, 1969) suggests that the ratio is low. Thus the ability to recover from damage may be subject to variation.

A study of the occurrence of *Melampsora* on progenies of *P. silvestris* shows that, with few exceptions, the attacked pines have longer terminal shoots than healthy pines of the same progeny (Klingström, 1969). Damage to terminal leaders is also much more common than damage to first whorls. This indicates that there can be a relationship between growth regulating substances and the occurrence of *Melampsora*.

Initial tests have shown that uninfected pine clones of varying susceptibility to pine twist rust can contain greatly differing quantities of preformed inhibitors in the annual shoots. Several acid substances that are soluble in ether have a strong inhibitng effect on *Melampsora* basidiospore germination. The substances in the extracts have been separated by gel filtration combined with thin layer chromatography (Klingström, 1969). In addition there are probably resistance reactions which are triggered by the combination of parasite and host, but no reports on this have been published in the case of *M. pinitorqua* on pine.

PERIDERMIUM PINI

BIOLOGY OF AUTOECIOUS AND HETEROECIOUS RACES

The blister rust of *P. silvestris* in Europe can be described as a *Cronartium* complex - *C. flaccidum* (Alb. & Schw.) Wint. (= *C. asclepiadeum* (Willd.) Fries). In this complex there are at least three races: *C. flaccidum* with a great number of alternate hosts, among others *Cynanchum vincetoxicum* (L.) Pers. and *Paeonia* spp.; *C. gentianeum* Thum. with *Gentiana asclepiadea* L. and *Paeonia* spp. as alternate hosts; and *P. pini* (Willd.) Kleb. (= *P. pini* (Pers.) Lév.) as an autoecious race.

This is not the place to discuss final scientific naming, but some further reports on *P. pini* will be quoted. There are no obvious morphological differences between host-alternating and pine-to-pine races. Since full-scale inoculation tests are extremely time consuming and are

frequently disturbed by resistance factors, attempts to discover other types of differences between the races are of great interest. In this connection primary attention is directed to Hiratsuka's work (1968), concerning morphology and cytology of aeciospores and germ tubes. He describes the host alternating race as binucleate with dichotomous germ tubes which lack septa. The aeciospores of the pine-to-pine race are described as uninucleate to some extent (16 to 28%) and with septa in the germ tubes. This information could be used as a complement to inoculation tests.

As far as the pine-to-pine race is concerned, the normal distribution biology has not been clarified. During my own field tests I have sometimes noticed that the aecia have been consumed by unidentified insects. The idea that insects might play a part as vectors is not a new one, but that they should be directly responsible for consuming the spores has not earlier been reported. Attempts were also made to bring some common Swedish insects--*Hylobius abietis* L., *Pissodes* spp.--into contact with aeciospore-bearing plants. These insects preferred the spore-bearing and enlarged spindleshaped part of the pines.

These reflections concerning insects led to tests for amino acids. The spores of the two types of rust differ in amino acid content. The analysis is simple where one has access to equipment for high voltage electrophoresis. Amino acids in spores or homogenized pine tissue were extracted in 96% ethanol. The free amino acids in the ethanol were separated at +38°C on paper (Munktell 302, 100 cm x 36 cm), using a formic-acetic acid buffer at pH 2 (25 g and 78 g to 1 *l* H_2O) and an operating potential gradient of 50 v per cm for 2 hours.

Bark tissue that has been attacked by *Peridermium* contains more amino acids than does corresponding healthy pine tissue. Attention has been directed primarily toward lysine and arginine, but the content of all amino acids is greater in attacked tissue. Spores from the two races of the fungus have also shown differences in the same group of amino acids. *Peridermium* spores have given a distinct reading for lysine and arginine, but this is absent in the samples from the host-alternating *Cronartium*. Needless to say, this can only be regarded as an indication of the differences that can exist, and the question must be examined employing more extensive material.

RESISTANCE BIOLOGY

Regarding *Peridermium*, the author has made a large number of crossings between infected (*Peridermium* trees), infected and healthy (Plus trees), and healthy pines. From this material a few crossings (table 1) have been selected as a complement to my earlier paper on inoculation.[1] These illustrate the current values concerning infection of pine progenies from crossings made as outlined above.

[1] *See A. Klingstrom elsewhere in these proceedings.*

Table 1. Percentage of seedlings from crosses of various *P. silvestris* parent trees showing cankers 14 months after inoculation with *P. pini*

Crosses	Number of seedlings	% cankered	Resistance ranking
Healthy S 6226 x Healthy S 6205	207	8.7	High
Healthy S 6205 X Infected A	234	5.9	High
Healthy S 6205 X Infected B	172	8.7	High
Healthy S 6205 X Infected C	206	9.7	High
Healthy S 6226 x Infected A	173	18.5	Medium
Healthy S 6226 x Infected B	174	14.9	Medium
Healthy S 6226 X Infected C	209	19.6	Medium
Infected B X Infected A	116	21.5	Medium
Infected C X Infected A	205	29.2	Low

Shoots surrounding the terminal leader of 3-year-old plants were inoculated with 2 spore samples of different geographical origin. The percentage values refer to the total percent cankering from both spore samples. The same pine is rarely receptive to both inoculations. Different pine progenies can thus vary in their degree of sensitivity to *Peridermium*, but also *Peridermium* from different sources shows a certain variability. This means that the choice of spores must be subject to continuity. It can also be questioned how many and which types of spores should be used in the tests.

SUMMARY

M. pinitorqua is a common parasite on a number of European pines. Also many introduced American pines are susceptible.

The establishment of the fungus on pine shoots depends on damp weather conditions favorable for basidiospore formation during the axial extension of succulent pine shoots. But it has also been proved that pine shoots contain several substances that have an inhibiting effect on *Melampsora* basidiospore germination. Other inhibitors have been traced in leachates from the surface of pine shoots.

Pine material with differences in susceptibility to attack by *Melampsora pinitorqua* has been described, but there is as yet no breeding work using this material. And the question of how to score attack by the twist rust in an acceptable way for routine work is still to be solved. There are no obvious morphological differences between host-alternating *Cronartium* and *P. pini*. Attention is drawn to cytological

differences in aeciospores and germ tubes, and to indications of differences in amino acid content of aeciospores of the different strains of the fungus.

An account is also given of an inoculation experiment with different *P. silvestris* progenies with varying degrees of susceptibility.

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FLOOR DISCUSSION

Discussion of the above paper appears after the paper by Dr. Steenackers that follows.

THE STATE OF KNOWLEDGE IN BREEDING RUST RESISTANT POPLARS

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ABSTRACT

The different poplar rusts, which are among the most dangerous poplar diseases, produce similar disease symptoms all over the world. Lists of the different rust species have been published by several authors. At the moment some confusion still exists concerning the identity of the different rust species, the alternate host plants, the poplar species and clones affected by each rust species, and the geographical distribution of the rust species.

Normally the different *Melampsora* species have two host plants. Van Vloten has proved the existence of different physiological strains of *M. larici-populina*. A more accurate identification of the different rust species is possible normally only by means of pathogenicity tests on the two host plants. In their native localities the four main poplar species *P. nigra*, *P. deltoides*, *P. trichocarpa* and *P. maximowiczii* can be attacked by one group of rusts, and once they are introduced to another area by a different group of rust species.

Field testing of poplar reaction to rust is very easy if only one poplar rust species occurs in the area for which the poplars are bred. And in western Europe, even if in the test country two or more rust species occur, different clones of *P. deltoides* and hybrids *P. deltoides* x *P. nigra*, *P. deltoides* x *P. trichocarpa*, *P. deltoides* x *P. maximowiczii* are available that have remained virtually immune to rust for many years. From the practical breeding point of view, this field testing method is useful and important, especially if the clonal reaction towards the different rust species is emphasized.

So far the breeding of rust-free poplars in western Europe is completely based on the highly resistant *P. deltoides* parent clones. F_1 and F_2 offspring of *P. deltoides* have been obtained which are completely free of rust symptoms.

More accurate information concerning the rust species involved, the typical reaction of each clone to each rust species, the heritability of rust resistance, and the number and kinds of genes involved can only be obtained from controlled inoculation tests using clearly identified rust species and poplar clones, in well isolated growth chambers or greenhouses.

INTRODUCTION

Melampsora species (Basidiomycetes, Uredinales), from all over the world, produce similar disease symptoms on the leaves of species and hybrid poplar clones. The rusts are without doubt among the most dangerous poplar diseases. Many examples are reported in the literature of heavy rust infections which result in early defoliation, reduction of growth, and even dieback of young and old trees.

At the same time, an early leaf fall has a marked influence on the infection of the tree by *Dothichiza populea* Sacc. & Briard. Even if it is possible to fight the disease by spraying with fungicides, breeding resistant clones by selection and hybridization is by far the best and cheapest way of controlling the disease in nurseries and plantations. This paper deals with the state of knowledge in breeding of rust-resistant clones of the poplar species *Populus nigra* L., *P. deltoides* Bartr., *P. trichocarpa* Torrey & Gray ex Hooker, *P. maximowiczii* Henry, and the reciprocal hybrids.

RUSTS OF POPLARS--GEOGRAPHICAL DISTRIBUTION

Based on field observations or artificial infection tests, different authors have published more or less complete lists of the rust species, their aecial and uredial hosts and their geographical distribution.

A list for the Netherlands, based on his own observations, has been published by Gremmen (1954). Another list is given by Peace (1962). Hennebert (1964) and Veldeman (1964) have published lists of the most common rust species occurring in Belgium. A more recent list for France is published by Taris (1966) in his handbook "Poupliers et Populiculture".

In Canada, Ziller (1965) has made controlled inoculation experiments with rust species on various host plants. One conclusion of this work was that *Melampsora albertensis* Arth. would be reduced to synonymy with *M. medusae* Thüm.

According to various authors clones of *P. nigra*, *P. deltoides*, *P. trichocarpa*, *P. maximowiczii* and the reciprocal hybrids are affected in different degrees by the various rust species. But there always exists a certain confusion concerning the identity of the rust species, the alternate host plants, the poplar species and clones affected by each rust species. Also, the geographical distribution of the rust species is not always clear.

MELAMPSORA ABIETIS-CANADENSIS (FARL.) C. A. LUDWIG

Following Peace (1962), this rust lives on *Tsuga* spp., aspen (*P. tremuloides* Michx.), and white and balsam poplars, in North America.

MELAMPSORA ALLII-POPULINA KLEB.

The aecia are formed on different *Allium* species. According to Peace (1962) and Taris, this rust affects black and balsam poplars. Gremmen (1954), in the Netherlands, has isolated this rust only on Section *Aegeiros* Duby poplars. Veldeman (1964) isolated it in Belgium from

P. trichocarpa and from the hybrid *P. trichocarpa* x *P. nigra*. According to Taris, this rust is limited to Asia while Peace (1962) reports that it is found in North Africa and Argentina as well.

MELAMPSORA LARICI-POPULINA KLEB.

The aecia are formed on different *Larix* spp. Peace (1962) reports this rust occurs in Europe, the Near East and Argentina. According to Taris, it exists in Eurasia, North Africa, North and South America. A high number of clones of the four main species and their hybrids are susceptible to this rust.

MELAMPSORA MAGNUSIANA WAGN.

Chelidonium majus Lour. and *Corylus* spp. are the aecial hosts of this rust which, according to Peace (1962), is limited to aspen and white poplars in Europe and Japan, but, according to Taris also affects *P. alba* L., *P. tremula* L., and *P. nigra* in Europe.

MELAMPSORA MEDUSAE THÜM

The aecial spores are formed on *Larix* spp. Peace (1962) reports black and balsam poplars are susceptible to this rust in North America and France, while Taris does not mention this species for France.

MELAMPSORA OCCIDENTALIS JACKS.

This rust is found in North America on black and balsam poplars.

MELAMPSORA ROSTRUPII WAGN.

The aecial spores are formed on *Mercurialis perennis* L. Gremmen (1954) isolated it on white poplars. According to Peace (1962), it occurs on white poplars and only rarely on black and balsam poplars in Europe. According to Taris, *M. rostrupii* affects a large series of species and clones of white poplars, *P. balsamifera* Muenehh., *P. nigra* and many different euramericana hybrids in Europe but rarely in North America.

NORMAL LIFE-CYCLE OF POPLAR RUSTS

The species of *Melampsora* normally have two host plants. The uredia and the telia are formed on the poplar leaves, whereas the aecia are formed on an alternate host.

The orange or yellow uredia occur in midsummer, usually on the under surface, but sometimes on the upper surface of the poplar leaves. The uredospores infect other young poplar leaves and are responsible for the quick spreading of the disease all over the nurseries and plantations. The brown telia are formed in the autumn, mostly on the upper side of the poplar leaves. The sporidia infect the alternate host and yellow aecia appear during late spring. Even in our experimental nursery, where for some years very susceptible poplar plants have been interplanted with

Larix, the aecia of *M. larici-populina* are sometimes rather difficult to find.

Through laboratory experiments, Taris showed that uredospores of *Melampsora* spp. can maintain viability and pathogenicity for 10 months. In this way, he reported, the uredospores assure the perpetuity of the rust species without passing through the aecial host.

Toole (1967) identified the common rust on *P. deltoides* in the Lower Mississippi Valley as *M. medusae*, which year after year, survives without the presence of a larch host.

Ge (1964) has described the symptoms of *M. rostrupii* on *P. tomentosa* Carr. in China, but the alternate host was not found.

According to the observations of Gremmen (*personal communication*), only a few uredospores will survive in nature once the poplar leaves drop and the teleulostage starts. The small number of surviving uredospores in nature will very quickly deteriorate due to changing temperature and moisture conditions. However, the number of viable uredospores, on the leaves, grown under artificial conditions is much higher.

PHYSIOLOGICAL STRAINS OF POPLAR RUSTS

While there is no information concerning the existence of geographical races of the poplar rusts, van Vloten (1944) has proved the existence of different physiological strains of *M. larici-populina* in the Netherlands. It is possible to differentiate the strains by comparing the reaction of a series of poplar clones to these strains after artificial infection. At the same time, van Vloten showed that new virulent strains can originate by crossing of two different strains.

More recently, two physiological strains of *M. allii-populina* were isolated by Magnani (1965).

IDENTIFICATION OF POPLAR RUSTS

Several authors have made observations and measurements of the color, form, and size of the different fruiting bodies, of mycelium, spores, and paraphyses on both host plants of several rust species.

Gremmen (1954) and Taris have made many measurements of the different spores and especially of the paraphyses in the uredosori of *M. allii-populina* and *M. larici-populina*.

Hennebert (1964) prepared two dichotomic keys to facilitate identification of the rust species. One key is based on form and size of the uredospores; the other is based on the teliospores.

Most authors have concluded that it is difficult, if not impossible, to identify a poplar rust solely by morphological characteristics of the spores.

Accurate identification of the rust species is normally possible only by means of pathogenicity tests on the two host plants. However, certain morphological characteristics, and eventually the color of certain spores are helpful. In the inoculation tests, it is necessary to use only

monosorus isolates of spores. To avoid possible natural infection by the spores of another rust species, it may be necessary to isolate the inoculated plants in a greenhouse.

The technique of these different inoculation tests is described by van Vloten, Gremmen, Chiba, and Taris.

Several workers have used artificial inoculation tests to identify the rust and to test the reaction of different poplar clones to this rust.

BREEDING AND TESTING OF RUST-RESISTANCE OF POPLARS

The pure species are, without any doubt, the most useful basic material for a long-term breeding program of new poplars. The aim of such a program must first be to incorporate resistance to the most important diseases into the species and clones of poplar. To be most successful this must be done all at the same time.

Because it is difficult to find resistance to the major diseases in only one species, interspecific crosses are at least as important and necessary as intraspecific crosses. It seems however that certain interspecific crosses are very difficult, or even impossible, to make. In spite of numerous pollinations with different parent trees, we have never successfully crossed *P. nigra* x *P. deltoides*.

Even crosses between three separate species are useful in breeding new clones with an increased resistance to different diseases.

Regarding rust resistance, it is necessary to test the reaction of the parent trees and their offspring to the native rust species.

FIELD TESTING OF THE REACTION OF POPLARS TO ONE RUST SPECIES

If only one poplar rust species occurs in the area for which the poplars are bred, the testing system is usually very simple.

The easiest procedure in this case will be to interplant poplar clones with plants of the alternate host in one nursery. To stimulate and create epidemic conditions, it is very effective to scatter, during springtime, heavily infected leaves of highly susceptible poplars over the ground of the experimental plot. Epidemic conditions can also be created during the summer by spraying the poplar leaves of the test clones with distilled water in which fresh uredospores are suspended.

Jokela (1966) has worked more or less in this way to test the reaction of different lots of seedlings of *P. deltoides* in Illinois to *M. medusae*. And, Chiba in Japan tested the variation of susceptibility of 121 different clones to *M. larici-populina*, under nursery conditions.

The results obtained by Jokela (1966) and Chiba have clearly shown that different poplar clones differ in their degree of susceptibility to the respective rust species. Later on, Chiba confirmed the results of the field tests by artificial inoculations in the greenhouse.

FIELD TESTING OF THE REACTION OF POPLAR CLONES TO DIFFERENT RUST SPECIES

Under certain conditions, a similar, but not equivalent testing method can be used if two or perhaps more rust species occur in the test country.

So far, there is no complete information concerning the geographical distribution of the rust species in Europe. We know that different species can occur in the same locality, perhaps on the same tree and on the same leaves. We have at the moment seedlings of the cross between *P. nigra*, Wannebecq 2 x *P. nigra*, Ollignies, which are probably infected by two rust species.

In one experimental nursery, there exist several clones of poplar species with extremely different degrees of susceptibility to rust. These clones have been present in the experimental nursery for many years. And several rust species were probably present. From our experience, even in these conditions of high natural infection, different clones of pure *P. deltoides* and hybrids *P. deltoides* x *P. nigra*, *P. deltoides* x *P. trichocarpa*, *P. deltoides* x *P. maximowiczii*, remain completely immune to rust every year.

Moreover, once the selected immune clones are transplanted in experimental plots all over the country, these clones remain immune. Some clones have already remained immune for 20 years.

From a practical breeding point of view, this field testing method is useful, at least for the immune clones. It permits yearly testing of large numbers of seedlings in a very short time and at very low cost.

ARTIFICIAL RUST INOCULATION TESTS

More accurate information concerning the rust species involves the determination of the typical reaction of each clone to each rust species, and the heritability of rust resistance. These can only be obtained through artificial infection tests in well isolated boxes or greenhouses.

From a practical breeding point of view, artificial inoculation tests on the clones which seem to be immune in field test to the local rusts, are not at all urgent and even not always necessary. On the other hand, the artificial inoculation tests are indispensable on those species and clones which, in field tests, show varying degrees of susceptibility to one or more local rust species, but which show other characteristics of much value to a long range breeding program. For example, clones of *P. nigra* in western Europe vary in their susceptibility to rust, but are highly resistant or immune to bacterial canker (*Aplanobacterium populi* Ridé).

Up to now, however, this artificial testing method has been applied by few workers and only on a restricted number of clones of the species and hybrids.

REACTION OF FOUR IMPORTANT POPLAR SPECIES TO SEVERAL RUST SPECIES

POPULUS NIGRA

When we group the observations and information of various authors in Europe, it seems that *P. nigra* in general is susceptible to many rust species, and more particularly to:

M. larici-populina
M. allii-populina
M. rostrupii
M. magnusiana

Looking at the impressive list of rust species affecting the species *P. nigra*, it is not at all surprising to note that all the different *P. nigra* clones examined up to now are, to a certain degree, susceptible to rust in the European conditions.

Little information is available concerning the reaction of *P. nigra* to the North American rust species.

On the trees of *P. nigra fastigiata* which we examined during a study tour in the Mississippi valley, we never detected the uredospores of rust, whereas the seedlings of *P. deltoides* growing near the *P. nigra* trees, were susceptible to rust.

Chiba found variation in susceptibility of some clones of *P. nigra* to *M. larici-populina* in Japan, in both field tests and by artificial inoculation. In practice, however, it is difficult if not impossible to test by artificial systems the reaction of many thousands of seedlings of *P. nigra* to different rust species.

The selection of the more rust-resistant *P. nigra* clones has therefore been based almost solely on repeated observations under field conditions. According to different rating systems, the rust-susceptibility is scored in the field three to four times a year, for several years.

In 1959, we discovered the last surviving *P. nigra* trees of Belgium. During the years 1960 to 1964 we produced 25,000 seedlings from 75 different full-sib families. Controlled pollination between the best of these trees hopefully will rebuild the native *P. nigra* population. So far, 2,500 seedlings have been selected and transplanted.

POPULUS DELTOIDES

According to different authors, *P. deltoides* in its natural range can be affected by at least two different rust species, *M. medusae* and *M. occidentalis*. Two percent of the native population of Illinois appear to be highly resistant to *M. medusae* (Jokela, 1966).

Toole (1967) identified the common cottonwood rust in the Lower Mississippi valley as *M. medusae*. But it is not yet known how this rust persists year after year, without the presence of a larch host.

During the last 20 years, seeds of many different origins have been distributed to the European poplar research centers by American colleagues.

As far as we know at the moment, *P. deltoides* in Europe can be affected by *M. larici-populina* and *M. allii-populina* (Gremmen, 1954; Magnani, 1965; Taris; Veldeman, 1964). Only a very restricted number of clones of *P. deltoides* have been artificially inoculated with the spores of these two rust species.

On the basis of field observations over several years on the same *P. deltoides* clones but planted on different sites, we concluded that for nearly every origin, there was a complete range of variation in reaction to the different European rust species, going generally from extremely susceptible to very resistant and even to immune clones (Table 1). Only the percentage of trees following the different reaction types, differ from one origin to another.

Table 1. Percentage of infected seedlings of *Populus deltoides* based on numerous field observations from 1954 to 1968

Collection number	Provenance	Number of seedlings	% completely free of rust
S.620	Michigan	1751	64
S.621	Iowa	724	68
S.622	Iowa	232	75
S.623	Iowa	103	71
S.264	South Dakota	151	32
S.626	Connecticut	752	3

The selection of *P. deltoides* clones resistant to the European rusts is not difficult. Even if the reaction of every clone to every rust species is not tested separately by artificial inoculation tests, we may speculate that specimens among the newly selected clones are completely resistant and even immune to the rust species occurring in western Europe.

POPULUS TRICHOCARPA

According to different authors, this species is susceptible in North America to three rust species, *M. abietis-canadensis*, *M. medusae* and *M. occidentalis*. Because of the confusion that still exists in Europe concerning the identification and the nomenclature of the balsam poplars, a good survey of the literature concerning the reaction of *P. trichocarpa* to the European rusts is difficult. In summary it seems that the species can be affected by *M. larici-populina*, *M. allii-populina* and *M. rostrupii*.

At least in Europe, a few artificial inoculation tests have been made on clones of *P. trichocarpa*.

The different clones under field test, in the experimental plantations of Europe, are, without exception, susceptible to one or more rust species. In most cases the rust species was not identified. However, it has been shown many times that different clones, even those belonging to the same full-sib family, show a pronounced difference in susceptibility. In our cross S.724 (V.235 *P. trichocarpa*, Washington x V.24 *P. trichocarpa*, Oregon), rust scoring varies from 2 to 5, on a scale of 1 to 5.

Recently we were successful in crossing the more resistant F_1 clones.

POPULUS MAXIMOWICZII

In Japan, *P. maximowiczii* is susceptible in nature to *M. larici-populina*. Chiba has tested the reaction of 27 different clones of *P. maximowiczii* to this rust by field tests and artificial tests in the greenhouse. Two clones were more resistant than the others.

In North America, *P. maximowiczii* is susceptible to *M. medusae* (Berbee, 1964).

In Europe, all the imported clones of *P. maximowiczii* are susceptible to *M. larici-populina* and perhaps to some other rust species.

From the breeding point of view, it is extremely important to emphasize the clonal reaction towards each rust species. For each of the four species, it is possible to select for resistant and even immune clones. The best result in the breeding of rust-resistant poplars can be obtained by crossing the most resistant clones of every species.

HEREDITY OF RUST RESISTANCE

Following Jokela (1966), resistance to *M. medusae* is a highly heritable feature in eastern cottonwood in the U.S.A. At least 2 percent of the native populations of *P. deltoides* appear to be highly resistant to this rust in Illinois, Consequently, considerable gain in rust resistance can be obtained in using these highly resistant clones in plantations and in breeding work.

The clones of *P. nigra, P. trichocarpa* and *P. maximowiczii* are, without exception, susceptible in Europe to one or more rust species, but some clones of *P. deltoides* remain free of rust. These rust-free clones of *P. deltoides* are selected in an empirical way, based solely on frequently repeated field observations.

Crosses between two such *P. deltoides* clones, made here in Belgium, frequently gave a high percentage of seedlings free of rust symptoms. In particular crosses we have obtained F_1 and F_2 generations in which all the seedlings are completely free of rust symptoms. This is true at two sites (at latitudes 45° and 51°) for the F_1 and F_2 generations of the following crossings: S.666 = V.8 *P. deltoides*, Missouri x V.12 *P. deltoides*, Illinois, and S.748 = V.9 *P. deltoides*, Missouri x V.9 *P. deltoides*, Missouri. It seems that these *P. deltoides* clones are highly resistant to several rust species.

Crosses between rust-free and rust-susceptible clones of *P. deltoides* give in the offspring a number of seedlings free of rust varying between 20% and 80% according to the parent clones involves.

This percentage of rust-free seedlings varies for the numerous crosses made between rust-free clones of *P. deltoides* and rust-susceptible clones of *P. nigra* or *P. trichocarpa* or *P. maximowiczii*.

Hybrid clones of rust-free interspecific crosses are more resistant to different rust species, whereas hybrid clones of rust-susceptible interspecific crosses are susceptible in varying degrees. We have never obtained a single seedling completely free of rust symptoms in the intra- or interspecific crossings involving rust susceptible parents of the above four poplar species. However, clones with low resistance have been selected in the F_2 generations of intraspecific crossings between *P. trichocarpa* and *P. nigra*.

Even if breeding rust-resistant poplars is based only on empirically repeated field observations, the results are very useful. However, a long-term breeding program will require more precise information concerning the heritability of rust resistance and the number and kinds of genes involved.

This will necessitate a complete analysis of the reaction of offspring of different successive intra- and interspecific poplar crossings to the various rust species, by means of artificial inoculation tests in the greenhouse.

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FLOOR DISCUSSION

(Also covering preceding paper by Allan Klingström)

ZUFA: I have two questions. Dr. Klingstrom, is the heritability of the resistance against *Melampsora pinitorqua* known? Dr. Steenackers, does the resistance of the same clones change in different environments or if confronted with different species or races of rust?

KLINGSTROM: Not very much is known about the inheritance of resistance to *Melampsora pinitorqua*. The only thing I can say is that a difference seems to exist between clones and progenies. The inheritance from parent clones to progenies has not been studied very much.

STEENACKERS: Well, in the first place we have tried to select clones that were completely free of rust. And then we tried to plant these clones on different sites in Belgium and at different latitudes, for instance, 45° latitude in the southern part of France, 51° and 52° latitude in Belgium. The clones that were completely free of rust, in our nursery in the beginning, still are completely free of rust at the various sites. Now I believe that most of the rust species are likely to be represented everywhere in western Europe because the host plants are present throughout western Europe. For the past 5-6 years we have been testing clones that are more or less susceptible. These susceptible clones score one or two, we have planted these clones at two latitudes. And after 5 years the susceptibility of the clones remained the same, but there is a difference in the degree of attack. The clones are less infected at 45° latitude in southeast France and more infected at 51° latitude in Belgium. Some of the clones have been observed for 15 years and still there is no change in susceptibility.

SCHREINER: I would just like to point out that the specific name *Melampsora medusae* has no real meaning any more for the U.S., and I doubt very much whether we have any area where we have a single species. I know in the northeast we have at least four. This is based on observations over many years of the alternate host. I have come to the point where I no longer use the specific name *medusae*. I simply say *Melampsora* spp. I did want to point out that there are many species and perhaps many more than you have in your own country.

STEENACKERS: I thank you very much, Dr. Schreiner, for this information and I hope these species will never come to Europe.

KINLOCH: With respect to the mechanisms or modes of inheritance to these various species, Muhle-Larsen reported in the world consultation on forest tree breeding in Stockholm, monohybrid and di-hybrid ratios in certain clones and hybrids and presented evidence for simple inheritance of resistance. The species of rust were not explained nor were the techniques of evaluation. I wonder if you have any knowledge or comments to make on this.

STEENACKERS: To do studies on heritability you need susceptible seedlings in the offspring. You can only do these studies on crosses like *Populus deltoides* which is completely rust resistant times a *P. deltoides* which is susceptible. Now if, for instance, the offspring were, let us say, 20% rust infected and 80% noninfected you would still have to know to which species of rust the 20% infected seedlings were susceptible. And as far as I know, no one has done this type of work yet. Again I would like to say as Dr. Schreiner has said to us that in most places we have several rust species and we have got to isolate and identify each rust species on the seedlings. It is not possible to say what the heritability will be because the heritability will not necessarily be the same for the various rust species.

KINLOCH: I agree, and that's exactly why I asked the question, because it was not clarified in Muhle-Larsen's paper.

WEISSENBERG: I would like to know if there is any information on the resistance of *P. tremuloides* to various *Melampsora* species? This would be of particular interest to the Scandinavian countries. Is there any information on *Populus tremuloides* from United States or Canada in this respect?

HEIMBURGER: Yes, we have abundant information on that in Canada. We have in former years imported *P. tremuloides* from the west, from the prairies, from Colorado, and from British Columbia. And as soon as we move these east we get very heavy infection with the so-called *Melampsora medusae*. Some *Populus alba* clones are free from rust and the resulting hybrids are also free from rust. There is some dominance of resistance in *P. tremuloides* x *alba* crosses. *Populus grandidentata* Michx. is usually very susceptible to rust and in fact I sent some *P. grandidentata* to Dr. Peace in England and he found it was very susceptible to *M. pinitorqua*. *Melampsora pinitorqua* is of great potential danger to northeast North America because red pine (*P. resinosa* Ait.) and *P. grandidentata* grow together and it's a wonderful chance for *Melampsora pinitorqua* to go there and raise hell.

A BRIEF CONSPECTUS OF PATHOLOGY AND GENETICS OF *CRONARTIUM RIBICOLA* AS RELATED TO RESISTANCE[1]

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ABSTRACT

Infection of the pine needle by *Cronartium ribicola* results from the formation of infection structures in the substomatal chamber. The infection capability of a spore may be the result of an interaction of inherited tendency toward a specific type of germination with microclimatic influences on the host substrate. Although germination of basidiospores may occur within a relatively wide range of environmental conditions, the formation of infection structures and consequent infection of the pine are apparently subject to additional subtle factors such as fluctuating temperatures and a contact or chemical stimuli, or both, in the stoma of the pine needle.

Evaluation of clonal or progeny inoculation tests must include consideration of factors affecting host susceptibility, including age of stock, its genetic resistance or susceptibility, vigor of the trees, and maturation of tissues at the infection court.

Resistance in the pine host is expressed against initial infection in the needle, and against invasion and establishment of the fungus in bark tissues. Bark resistance is expressed by wound periderm formation or a hypersensitivity reaction. In the needle, stomatal influences play a role in the incidence of infection. Wax plugs appear to reduce the number of chances for infection to occur, especially in secondary needles, and may be one influence of age of stock, but probably this is not a major mechanism of inherent resistance. Inhibition of vesicle formation is another aspect of stomatal influence and is one way in which resistance to needle infection is expressed.

Inheritance of resistance seems to be largely through polygenes with additive effects. Information is just beginning to accrue on the numbers and kinds of genes associated with specific resistance reactions.

It is not yet known with certainty whether the fungus is homothallic or heterothallic, and if pathogenic races for pine exist.

[1] *Published with the approval of the Director, Wisconsin Agricultural Experiment Station. Supported in part by U.S. Forest Service Grant No. 1 (4000) and National Science Foundation Grant GB-3297.*

Breeding for resistance to white pine blister rust, incited by *Cronartium ribicola* J. C. Fischer ex Rabenh., appears to be the most practical approach toward long-term control of this disease. Several programs are now actively directed toward the development of blister rust-resistant white pines in both eastern and western United States and in Canada. So it is appropriate to consider our present knowledge of the biology of this rust fungus in relation to resistance expressed by the pine hosts. Emphasis in this paper is placed primarily on selected elements of the infection process and the relationships of these and critical factors in the genetics of the pathogen to the expression of resistance by white pines.

THE BASIDIOSPORE

Since the basidiospore, or sporidium, is the infecting agent of the pine, considerable attention has been given to conditions influencing its production and germination. These conditions are probably most important in nature from an epidemiological standpoint, but also are important to the tree breeder in progeny testing, both in test plots with exposure to natural inoculum and under conditions of artificial inoculation. Although spore germination is a prerequisite for infection, unfortunately in progeny testing infection does not always follow spore germination. Variability in germination behavior of basidiospores and the influence of subtle microclimatic effects at the site of spore germination are some of the more important aspects of basidiospore behavior still to be clarified.

PRODUCTION OF BASIDIOSPORES

Some variation occurs in the reports of conditions necessary for teliospore germination and formation of basidiospores (Bega, 1959). York and Snell (1922) reported that basidiospores were fully developed 5-6 hours after teliospores were exposed to favorable conditions for germination. At the opposite extreme, Van Arsdel, Riker, and Patton (1956) found that 36 hours were required for germination of teliospores formed at a constant 16°C, and 42 to 48 hours for germination of basidiospores and infection of pine. Hirt (1942) calculated 11-1/2 hours as a minimum time for infection after basidiospores were cast on pines but more infection resulted during longer periods of favorable conditions. The variations in techniques used by various workers, from floating excised telial columns on water to exposing intact plants with infected leaves in a mist chamber, undoubtedly influence the time for production of basidiospores. However, the inherent variability of the fungus is perhaps readily expresssed by exposure to a variety of environmental conditions from the period of telial formation to casting of basidiospores. About 6 to 14 hours (Bega, 1959; Hirt, 1935) seem to be the range of time most commonly encountered for basidiospore formation. Moisture at 96 to 100% relative humidity (Hirt, 1935), or as a free water film, is necessary for germination in the optimal temperature range of about 12 to 20°C.

Viability of teliospores is affected by environmental influences, and marked variations in spore casts are produced by changing meteorological conditions (Hirt, 1942). In particular, the temperature at which the telial column was formed has a marked effect on the subsequent germination of the teliospores (Van Arsdel, Riker, and Patton, 1956). These effects could be of importance in progeny testing by artificial inoculation.

GERMINATION OF BASIDIOSPORES

Germination of basidiospores requires 100% relative humidty or direct contact with water and may occur within the range of above 0 to 20°C (Hirt, 1935), essentially the same conditions required for germination of teliospores. Germination *per se*, however, is not an accurate measure of response of basidiospores to external conditions, as indicated by Bega (1960). He noted that other factors were involved, including type of germination, vigor (length of germ tubes), the period involved, and the type and condition of the substrate. Most conclusions about basidiospore germination capabilities have been based on spore behavior, under relatively constant temperature and moisture conditions, on a water film or an agar surface. Deviations from such results might well be expected on pine needles under fluctuating temperature and moisture conditions in the field.

Three different types of germination of basidiospores have been seen on white pine needles: indirect germination with formation of a secondary basidiospore; direct germination with formation of one and up to seven thin, sometimes branched germ tubes; or direct germination by means of a single thick, somewhat irregular germ tube that did not branch or did so only rarely (Patton and Nicholls, 1966). In our experience all three types usually have occurred on the same needle along with ungerminated spores, although in some experiments one type occasionally was more prevalent than others. In fact, the type of germination has been extremely variable in inoculation experiments and spore germination trials. Such variation was not related to the type, age, or source of needle. Certainly, variation in germination on needles from different sources was not the reason for differences in amount of infection observed with increasing age of the pine host or with inherent resistance of a selection (Patton, 1967).

The role of indirect germination in nature is still undetermined. Hirt (1935) reported that germination of secondary basidiospores usually resulted in formation of germ tubes. Bega (1960), however, was able to carry secondary basidiospore formation on water agar through six generations, but indicated that on pine needles only very few (0 to 1%) secondary basidiospores were formed. This was taken as an argument that secondary basidiospore formation was a response to an unsuitable host or substrate. In some of our tests, however, up to 47% of spores cast on needles (in counts of 200 to 900 spores per test) have produced secondary basidiospores (Patton, 1967).

The relative significance of thick and thin germ tubes in terms of infection capability still is unknown, although observations so far indicate that penetration into stomata, formation of substomatal vesicles, and subsequent infection of the needle mesophyll result from growth of "normal" thin germ tubes (Patton, 1967).

Finally, equating conditions for basidiospore germination with infection is still not valid. It seems possible that individual spores have some inherited tendency to germinate in one way or another, but perhaps microenvironmental influences, such as minute variations in a water film on a needle surface, have the greatest effect in determining what type of germination occurs. One example of variation under experimental conditions may illustrate our lack of knowledge concerning spore behavior. Basidiospores were cast on a collodion membrane floating on water in a closed petri dish with diurnal fluctuation of temperature between 10

and 21°C. Germination patterns of different 4-hour spore casts varied. In one instance spores on one-half of the microscope field observed with a 6.5X objective had germinated with thin, long, branched germ tubes. On the other half of the field, and separated as if by an invisible straight-line barrier, almost all the spores had germinated to form secondary basidiospores. Presumably some subtle difference between these two portions of the membrane substrate or its immediate environment was enough to produce this distinctive difference in the type of germination among basidiospores in a relatively uniform spore cast. Thus, it is easy to conceive that the interaction of an inherited tendency plus a given microclimate on the surface of a needle or within a stomatal pit may determine the infection capability of a spore on an individual needle. This may also involve the ability of a spore to form infection structures, such as the vesicle and infection hyphae.

NUCLEAR CONDITION OF BASIDIOSPORES

Along with studies of germination morphology, investigation of the nuclear condition of basidiospores may help clarify the reasons for variability in germination behavior and possibly also the infection capability. Most basidiospores are uninucleate. Sometimes, but not always, during germination the spores are activated so that nuclear division occurs. Colley (1918) reported that division of the single nucleus of the basidiospore to form a binucleate basidiospore was quite common. In some preliminary work in Wisconsin we found that the spore may contain even 3 or 4 nuclei, after which one or more germ tubes are formed. Germ tubes and vesicles with at least 2 nuclei have been observed in germinating basidiospores on collodion membranes. The binucleate condition of basidiospores results not only from nuclear division of an originally uninucleate basidiospore, however. It may also result from binucleate cells of a promycelium, where perhaps a wall has failed to form after division of the fusion nucleus of the teliospore. Such spores have been seen still attached to the sterigmata. Whether germination behavior or infection capability of such binucleate spores differs from that of the usual uninucleate basidiospore is still unknown.

THE INFECTION PROCESS

An old question asked by Spaulding and Rathbun-Gravatt (1925) is still pertinent today, particularly in view of our efforts in breeding programs to separate resistant from susceptible individuals: why does not infection always occur when external conditions are apparently favorable to it? It seems to me that the more detailed knowledge we have of the infection process the closer we can come to answering this question, and the more certain we shall be that stock released as resistant will stand the test of time.

MODE OF PENETRATION

It seems clear now that, in most if not all cases, the fungus enters the pine needle through a stoma, and subsequently produces a substomatal vesicle and infection hypha (Clinton and McCormick, 1919; Patton and Johnson, 1966; Patton, 1967). Hirt (1938) gave a brief account, without illustration, of direct penetration of epidermal cells, but at the same time reported that substomatal vesicles were seen. Boyer (1962) had

drawings and one photograph of what he interpreted to be fine penetration hyphae through the cuticle of primary leaves or the hypocotyl, but never observed a connection between these structures and internal mycelium. Even Patton and Nicholls (1966) reported possible direct penetration. But all of these reports are now believed by this author to be artifacts or faulty interpretation of strain lines or other optical effects in the cuticle or cell wall.

Infection of very young and succulent stem tissue was reported as a result of artificial inoculations by Van Arsdel (1968). Susceptibility decreased with shoot age, and cankers appeared most rapidly on stems inoculated at the tender-shoot stage. The mode of penetration of such tissue has not been determined but, since stomata may occur on such shoots (Clinton and McCormick, 1919), it is likely that infection of such succulent tissue occurs in the same manner as in the needles.

PRODUCTION OF INFECTION STRUCTURES

In the pine needle the characteristic feature of stomatal penetration is the formation of a vesicle in the chamber beneath the guard cells. An infection hypha then develops from the vesicle and grows into the mesophyll tissue, where it branches to form a mycelium that ramifies between and within the mesophyll cells and eventually into the vascular core. Vesicles have very rarely been seen on the needle surface, but seem invariably to result when a germ tube passes between the guard cells of a stoma. No appressorium is formed by the penetrating germ tube.

Infection structures have also been observed by the author and his co-worker Pritam Singh (*unpublished data*) when basidiospores were germinated on artificial substrates, such as collodion or cellophane membranes floating on water. Two factors important in influencing the number of infection structures produced are fluctuating temperatures and the contact stimulus provided by the membrane. No vesicles were seen when spores were germinated at a constant temperature of 16° or 20°C in 100% relative humidity on water films on glass slides. Under the same temperature conditions, basidiospores germinating on collodion membranes produced typical long germ tubes. A few of these (less that 0.5%) developed vesicle-like swellings on the germ tube. These were terminal bulbous swellings that did not develop further or, in fewer cases, an oval swelling that developed a short infection hyphae. On collodion membranes in temperatures fluctuating between 4.5°C at night and 21 to 24°C during the day, vesicles were considerably more abundant and seemed more typical in shape and size of those formed in needles. In a representative experiment, counts of over 2,000 spores in each of two trials revealed 79 and 90% germination, 10 and 5% of germinated spores with vesicles, and 5.6 and 2.4% of germinated spores with vesicles that had developed infection hyphae.

The formation of infection structures by germinating basidiospores is apparently influenced by several factors. Since vesicles are not formed at all or only very rarely on glass slides, the germ tube apparently needs some sort of stimulus provided by the guard cells in the needle or by artificial membranes. The chemical composition of the membrane and the solution on which it is floating also influence vesicle formation and, especially, development of infection hyphae. Finally, a diurnal temperature fluctuation from about 4.5 to 24°C results in more and better-developed vesicles than when spores are incubated at a constant temperature of 16°C. These are all factors that might act on germinating spores on pine needles

in the field and have some significance to infection and expression of resistance.

VARIATION IN HOST SUSCEPTIBILITY TO INFECTION

The influence of age has many ramifications in a breeding and progeny-testing program. Patton (1961) found that susceptibility of eastern white pine to infection decreased with age. One factor in this is that the number of needle penetrations decreases markedly with increasing age of the tree (Patton, 1967). The greatest difference is noted between primary and secondary needles, but also the number of infections in secondary needles of inherently susceptible trees decreases as the age of the tree increases. The influence of age upon the expression of inherent resistance also has been shown in artificial inoculation tests of progenies from crosses of resistant parents (Patton and Riker, 1966). Inoculated 1-0 stock died within 2 years after inoculation whereas up to 45% of 4-year-old seedlings from the same progenies were resistant to infection.

The influence of age is also expressed through effects on maturation of plant parts. Van Arsdel (1968) showed that susceptibility of young stems decreased with age of the shoots. Straib (1953) suggested that formation of telia early in the season in one geographical area may enable infection of pine at a more susceptible stage than in another area where telia formed later in the season when pine tissues are more mature and presumably less susceptible. Although direct infection of young stems apparently is unimportant in nature, it might play a role in artificial testing programs. Conceivably, susceptibility of needles might change during the season. This change, along with differences in shoot susceptibility, might well be considered in comparisons of inoculation results from different areas, as in international test programs and where stock was submitted to cooperators in other regions or countries for testing.

One expression of host resistance is its effect on the number of needle penetrations. Penetration of the germ tube into the substomatal chamber may be reduced almost to zero in very highly resistant selections (Patton, 1967). In testing progenies of resistant selections it could be important to determine whether this was the only resistance mechanism or whether others might act at a later stage in disease development.

The influence of vigor on susceptibility of hosts to infection by obligate parasites is well known. Boyer (1967a) showed that susceptibility of white pine seedlings to infection by *C. ribicola* was related to vigor as indicated by dry weight. Seedlings of low vigor grown on two poor soils developed fewer infection loci than more vigorous seedlings that grew on richer soils. Awareness of such a quantitative response is important in evaluating results of artificial inoculations in progeny testing.

STOMATAL RELATIONS TO INFECTION

There is a body of observational evidence for the influence of age upon host susceptibility and the expression of resistance, but the mechanisms of this influence are unknown. Since entry to the needle is gained through the stomata, some attention has been given to stomatal influences. Hirt (1938) concluded that it was difficult to determine what relation, if any, stomatal activity may have to needle penetration.

He noted that, if entry depends on access to open stomata, a relatively large number of stomata are open to some degree at all times of the day or night and fungal invasion would be permitted at any time. Germ tubes grow at random on the needle surface without any apparent regard for stomata (Hirt, 1938; Patton, 1967). Although Hirt called attention to the waxy plugs in the outer stomatal pits, he did not determine whether they influenced infection. In observations of germinating spores on needle surfaces, we saw numerous germ tubes growing across the wax plugs. Similarly, on microtome cross sections of needles embedded in paraffin, we observed germ tubes that had crossed the stomatal pit, although the wax plug had been dissolved in processing. No germ tubes have ever been seen penetrating solid wax plugs, but have been observed growing into large crevices in the plug, or into stomatal pits lined with a wax layer but not completely plugged.

To determine whether wax plugs were related to age, we compared the numbers of stomatal pits occluded with waxy deposits in cryostat-sectioned fresh needles from different sources (Table 1). In this sample a much larger percentage of pits were open or partially open in primary needles of 2-1/2-month-old seedlings than in secondary needles of three other sources. This relationship corresponded well with a similar comparison of vesicles formed in needles of trees of different age and susceptibility (Patton, 1967). Thus, it appears that wax plugs often prevent growth of germ tubes down into the outer stomatal pits, and consequently reduce the number of opportunities for infection even of susceptible needles. This effect may well be one influence of age, but is not considered a major mechanism of resistance.

Table 1. Occlusion of outer stomatal pits by wax deposits in needles from trees of different ages

Needle type	Age and type of host	Total No. of pits observed	Percentage of pits		
			Open	Partially open	Plugged
Primary	2-1/2-month-old seedlings	634	69.1	17.5	13.4
Secondary	4-year-old seedling	699	10.0	15.8	74.2
Secondary	Graft of 40-year-old susceptible tree	1,254	3.1	7.9	89.0
Secondary	Graft of approximately 50-year-old resistant tree	901	2.0	6.8	91.2

Another aspect of stomatal influence on infection in relation to age was intial growth of germ tubes into the outer stomatal pits. We found that the number of germ tubes that entered the stomatal pit and grew down to the guard cells, without further penetration into the substomatal chamber, was considerably less in secondary than in primary needles (Patton, 1967). The chances for a germ tube to enter a stomatal pit may be reduced by wax plugs in secondary needles. But the failure of germ

tubes to continue growth and form a vesicle in the substomatal chamber has not yet been explained. This could be the result of interaction of inherent spore capability with an influence exerted by the guard cells of the host.

DEVELOPMENT IN THE HOST

Development of the fungus in needle tissue subsequent to penetration has been described for susceptible trees largely from the standpoint of the intimate relationship of fungus and host cells (Clinton and McCormick, 1919; Colley, 1918; Boyer, 1962; Hirt, 1964). Following penetration, a loose mat of much-branched hyphal tissue develops. Haustoria are formed in mesophyll cells but as the fungus proliferates, much of the mesophyll tissue disintegrates, and finally a dense sclerotium-like mass of compacted mycelium is formed. Eventually the fungus breaks through the endodermis, enters the vascular tissue, and grows down the needle from which it invades the cortical parenchyma of young stems (Boyer, 1962), or the phelloderm and adjacent phloem cells in older bark and subsequently deeper tissues of the phloem (Hirt, 1964). Hirt (1964) also followed in great detail further developments through the production of pycnia and aecia.

The most detailed observations of the cellular response to infection are those of Boyer (1962, 1964a) and Boyer and Isaac (1964). Cells containing haustoria show an increase in granularity of cytoplasm. As the diseased cell ages, there is a marked reduction in size and number of chloroplasts, the cytoplasm appears homogeneous, and finally the nucleus dissolves. At the same time osmotic and permeability changes occur (Boyer, 1962). Primary emphasis in these investigations has been given to a histochemical study of phenols in white pine. One of the characteristic features of infection in foliage cells up to one season old was fragmentation of the vacuoles in which the phenols are localized. Observations with the electron microscope indicated that fragmentation of the vacuoles involves synthesis of new membranes, and this was considered in relation to the possible role of phenols in resistance (Boyer and Isaac, 1964). There was no evidence, however, that phenols released by vacuolar fragmentation were toxic to the haustoria or the intercellular mycelium (Boyer, 1964a).

RESISTANCE TO INFECTION AND DEVELOPMENT

TYPES OF RESISTANCE

Experience in testing selections and progenies of white pines under conditions of both natural and artificial inoculation has indicated there is more than a single type of resistance to *C. ribicola*. For example, there may be resistance of the needles to initial infection and resistance of the phloem tissue of the stem to establishment and continued growth of the fungus (Boyer, 1967b; Hoff, 1966; Patton and Riker, 1966).

The appearance of needle spots that failed to develop further or to form stem infections was reported by Riker *et al.* (1943) as one indication of resistance. Trees with such spots were clearly inoculated and were thus not merely disease escapes. Such foliar resistance is believed to be of major importance in rust resistance in both eastern and western white pines (Hoff, 1966; Patton and Riker, 1966; Patton, 1967).

Resistance in the bark is illustrated by recovery from established stem infections. Struckmeyer and Riker (1951) described the anatomy of wound periderm that served effectively as a barrier to prevent the fungus from progressing further into the tissue and resulted in a final corking-out of the infected area. Degrees of resistance were associated with capacities of trees to differentiate a cork cambium. This type of resistance is observed commonly in both eastern and western white pines. The reaction was a commonly used criterion of resistance in testing parent selection and progenies of eastern white pine in Wisconsin's program (Patton and Riker, 1958; Patton and Riker, 1966), and the same reaction has been found in progenies from crosses in Heimburger's program in Ontario (Boyer, 1964b). The typical corking-out reaction has also been reported for western white pine by Bingham, Squillace, and Wright (1960).

An additional bark reaction was classified by Bingham *et al.* (1960) as a hypersensitivity whereby a necrotic sunken lesion develops at the base of an infected needle. This also is a common reaction of eastern white pine.

Hypersensitivity may also play a role in foliage resistance. According to Hoff (1966), Boyer reported a hypersensitive reaction in the foliage of a single *Pinus peuce* Griseb. specimen. Hoff observed a similar type of reaction in *P. armandii* Franch. needles, in which there was premature death in the epidermis and mesophyll, and in *P. monticola* Dougl., where there was evidence of host cell death in association with host cell proliferation.

Some or all of these types of resistance may be present in different selections. A low frequency of needle lesions is one major measure of resistance (Patton, 1967). When several other criteria, including that of being completely disease free, were used in judging resistance in progenies of crosses between resistant eastern white pine parents, the percentage of resistant trees in progenies of better-than-average resistance-transmitting selections ranged from 16 to 70%, compared with about 10% in the control group. Such criteria included needle spotting but no subsequent canker development, needle death but no resulting stem infection, development of a necrotic sunken lesion around the needle base (hypersensitive reaction in the bark), and corking-out of small incipient stem cankers with complete recovery (wound periderm formation) (Patton and Riker, 1966).

NATURE AND MECHANISMS OF RESISTANCE

Although the gross symptomatology of resistance reactions has been described, little is known of the biochemical mechanisms involved in the interaction between host and parasite in the expression of resistance reactions. Some indications have been given of the possible association of phenolics or growth regulators with resistance, but since this aspect of resistance is covered in another paper in this panel no further details will be given here. One area still deemed important for further study is the resistance reaction expressed by inhibition of vescicle formation through interaction of host and parasite at the guard cells of the stomata (Patton, 1967).

The growth in culture of cambial explants infected with *C. ribicola* (Harvey, 1967) suggests that axenic culture of the rust fungus may be a technique that will prove useful in studying the nature of the host-parasite relationship or the physiology and biochemistry of resistance, and in screening selections and progenies for resistance.

THE GENETICS OF RESISTANCE AND PATHOGENICITY

INHERITANCE OF RUST RESISTANCE

The experience of workers with both eastern and western white pines indicates that resistance is inherited in a polygenic manner (Bingham *et al.*, 1960; Heimburger, 1962). From some of their earlier work, Bingham *et al.* (1960) suggested that the heritability of rust resistance may be fairly high. Their figures for broad sense heritability were 0.87 and for narrow sense heritability 0.69 (later reduced to 0.60 - Hoff, 1966), and they estimated the genetic gain between F_1 and F_2 generations to be about 20 to 24%. Selection and screening procedures for both parents and progenies of eastern and western white pines have proved relatively efficient. But only about one in four tested selections of western white pine exhibited general combining ability for seed-transmission of resistance and about one in six of eastern white pines (Bingham, 1966; Patton and Riker, 1966). Additional information on heritablity of resistance in western white pine is included elsewhere in these proceedings.

The numbers and kinds of genes involved in white pine blister rust resistance are not yet well known, but most information at present points to the importance of genes with additive effects. Heimburger (1962) has suggested that *P. monticola* is less polygenic than *P. strobus* L. and that the former possesses a smaller number of resistance genes, each stronger in action. In some crosses of *P. wallichiana* A.B. Jacks. (syn. *P. griffithii* McClell.) with selected *P. strobus*, high proportions of seedlings free of blister rust indicated that major genes might be influencing resistance, probably through suppression of a (probably recessive) gene or genes, inhibiting growth of the rust from needles to stem. Bingham (1969) suggested that the association of specific resistance reactions with discrete resistance genes be a major topic for investigation in the near future. Additional data on identification of particular resistance genes are being prepared for publication in these proceedings or elsewhere.

SEXUALITY OF *C. RIBICOLA*

At the same time we are concerned with variability in the host, as expressed by host resistance, we must also consider the possibility of variability in the pathogen, particularly as expressed by variability in pathogenicity. Such variability is based first upon mutation, and new races commonly appear as the result of recombination of genes largely through sexual processes (Walker, 1963). If virulence of *C. ribicola* is subject to relatively rapid change by sexual means, it certainly would be extremely important to take that into account in our resistance breeding programs.

The reproductive phenomena in *C. ribicola* are still incompletely understood. Pierson (1933) reported a fusion of pycniospores with certain filamentous hyphae in pycnia of the rust on western white pine. Then Buller (1950) deduced that proper pycniospore exchange was necessary for aeciospore production, that the rust was heterothallic. Hirt's investigations, although they were still inconclusive (Hirt, 1964), presented evidence that conflicted with this belief. A major objective of Hirt's work was to determine whether exchange of pycnial exudate was essential to the production of aecia. Experimental limitations and certain assumptions necessary in his work allowed for the possibility of errors in his conclusions. His study of the formation of the pycnium

indicated that structurally it was not a very efficient organ for the reception of external pycniospores and their contact with internal flexuous hyphae. Also, under his conditions, aeciospores were produced without the exchange of pycniospores between pycnia on different cankers. He concluded that if heterothallism in *C. ribicola* requires the exchange of compatible pycniospores between pycnia prior to the formation of aeciospores, his results did not indicate the fungus to be heterothallic. Conclusive proof remains to be obtained by making pycnial exchanges between isolated cankers known to be of single-basidiospore origin, or by other approaches as noted by Bingham (1969).

RACES OF *C. RIBICOLA*

New races of such organisms as our tree rusts are probably being formed continually through mutations in pathogenicity and recombinations through sexuality, parasexuality, and heterokaryosis. The survival and increase of a given race primarly depend on the resistance of a host. A change in the host substrate, such as the sudden production of resistant trees, may lead to conditions favorable for a race that previously could not have survived or become important. We know that various biotypes of *Cronartium* species now exist, but we have no information on the likelihood or the speed with which a race could shift in prevalence.

There is some evidence that physiologic races of *C. ribicola* do exist. Hahn (1949) was unable to find evidence of pathogenic races on immune *Ribes* in Canada. Anderson and French (1955), however, reported differences in virulence as evidenced by a necrotic reaction on a clonal line of *Ribes hirtellum* Michx. between aeciospores collected from sugar pine in the West and those from eastern white pine sources in the East and Midwest. Differences in morphology of germ tubes of aeciospores from three different collections in neighboring white pine stands were considered as evidence of physiologic races by Straib (1953). Recently, Bingham (1969) reported finding different colored needle lesions resulting from *C. ribicola* infections on the same western white pine needle and plant. All of these findings point to variation in *C. ribicola*, but there is no knowledge yet of variation in pathogenicity on pine, the feature that is of most importance to our efforts in resistance breeding. Determining the existence of pathogenic races on pine involves difficulties in developing adequate methods for their detection. But as our understanding of the pathology and genetics of both the host and parasite increases, it is likely that we can obtain a more precise estimate than we now have of the possible impact of pathogenic races on the development of resistant white pine stock.

SUMMARY

The development of blister rust-resistant white pines depends to a large measure upon our understanding of both internal and external influences on the behavior of *C. ribicola*, as well as a knowledge of resistance in the host.

Infection is tied in closely with conditions influencing basidiospore production and germination. The production of basidiospores depends not only on conditions for teliospore germination but also on those during teliospore formation. Since infection does not always follow spore germination, further clarification is needed of the significance of

variability of spore germination and the influence of subtle effects of the microclimate at the site of basidiospore germination. The infection capability of a spore may be determined by interaction of an inherited tendency toward a specific type of germination with a given set of microclimatic influences on the host substrate.

Infection in the needle results from the formation of infection structures in the substomatal chamber. The production of infection structures is influenced by fluctuating temperatures, a stimulus provided by an artificial membrane, and a contact or other stimulus provided by the guard cells of a stoma. These are factors which apparently also influence infection of the pine needle.

In evaluating results of natural and artificial inoculations on clones and progenies, factors influencing host susceptibility, especially age of stock, inherent susceptibility or resistance of the stock, vigor of the trees, and maturation of tissues at infection courts are all of importance.

Both foliar resistance to initial infection and bark resistance to invasion and establishment of the fungus are known, but these have not yet been correlated with discrete resistance genes.

Little detailed information is available on the nature and mechanisms of resistance. Bark resistance is expressed by wound periderm formation or a hypersensitivity reaction. In the needle, stomatal influences play a role. Wax plugs appear to reduce the number of opportunities for infection, especially of secondary needles, and may be one influence of age but not a major mechanism of resistance. Inhibition of vesicle formation, even after growth of a germ tube into the outer stomatal pit, seems to be another aspect of stomatal influence on infection and resistance.

Inheritance of resistance seems to be largely through polygenes with additive effects. Information is just beginning to accrue on the numbers and kinds of genes associated with specific resistance reactions.

The possibility of pathogenic races on pine, of which there is still no evidence, emphasizes the importance of continued investigation of the sexuality of *C. ribicola*. There are now some indications that the fungus may be homothallic, but a more complete understanding of its sexuality and variability in pathogenicity for pines is necessary to assure continued success of our efforts to develop resistant planting stock.

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FLOOR DISCUSSION

Panel leader Schütt withheld discussion of this paper until after Dr. Kinloch's paper, immediately following.

GENETIC VARIATION IN RESISTANCE TO CRONARTIUM AND PERIDERMIUM RUSTS IN HARD PINES

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ABSTRACT

Among the four major and closely related species of southern pines, susceptibility to *Cronartium fusiforme* ranges from high to near immunity, with interspecies hybrids exhibiting a similar range. Inheritance of resistance in hybrid progenies is apparently complex and dependent on the genotypes of individual parents. Within species, a distinct pattern of racial variation in resistance exists in loblolly pine (*Pinus taeda*), but both that species and slash pine (*P. elliottii*) show even greater variation among individual parent trees. Heritability of resistance is high and relatively stable to varying conditions of rust hazard.

Evidence of resistance to other pine stem rusts is limited but similar. Racial variation in susceptibility to *C. quercuum* is evident in jack pine (*P. banksiana*), and both racial and individual tree differences in susceptibility to *Peridermium pini* are known in Scots pine (*P. sylvestris*).

Little is known of mechanisms of resistance to most of the pine stem rusts, though earlier work on *P. harknessii* indicated a physiological basis, depending on the rate of response of cortical tissues to invasion by rust mycelium. The most resistant reactions resulted from rapid necrosis of affected cells, similar to hypersensitive type reactions of other plant rusts.

Variation in pathogenicity on pines, one of the most critical problems, has been found in *P. pini* and *C. fusiforme*, but relatively few studies have been made. Potential variation depends largely on the sexual behavior and extent of gene exchange in the various rust populations.

New approaches to the analysis of genetic interactions between hosts and pathogens in wild, heterozygous populations are discussed in the context of the gene-for-gene theory and illustrated by a case study of another tree rust. Through knowledge and recognition of properties inherent in a complementary genic system, analysis of this host-parasite combination was possible in only one generation of breeding. The applicability of this type of approach to pine rusts is discussed.

Members of the genus *Cronartium* and *Peridermium* that attack pine stems are among the most destructive pests of forest trees. Of the 15 taxa recognized by Peterson (1967), several are currently epidemic in different parts of the world, and others are undoubtedly capable of becoming so. An obvious lesson from cultivated plants that is increasingly apparent in forestry is that disease problems amplify when a crop becomes domesticated. Endemic diseases of formerly minor importance can become major threats to their natural hosts and disastrous to introduced ones.

Fusiform rust was little more than a mycological curiosity until major reforestation programs started in the southern U.S.A. Now, in many areas of the South, it is the factor most severely limiting plantation management. Plantations in the Mediterranean area have been similarly affected by Scots pine blister rust (Biraghi, 1963), as have those in India by chir pine blister rust (Bakshi, 1963). Comandra rust was never a problem on loblolly pine until it was planted outside its natural range on the Cumberland Plateau in Tennessee, where it became victim to a serious epidemic (Powers, Hepting, and Stegall, 1967).

Sweetfern rust has ravaged exotic plantations of shortleaf and lodgepole pine in eastern Canada (Van Sickel, 1969), and Monterey pine in British Columbia (Molnar, 1961). It is morbidly fascinating to contemplate the fate of the latter species over millions of acres of exotic plantations in Australia, New Zealand, and other countries if its endemic and autoecious rust, *P. harknessii* Moore, ever became established. Although widespread epidemics of indigenous rust diseases in natural stands are unusual (Peterson and Jewell, 1968), a report of heavy outbreaks of cone rust in Guatemala suggests that they occasionally do occur (Schieber, 1967).

The need for sources of resistance to these rusts is obvious and urgent. But we know from experience with other rust diseases that resistance is often labile. Sustained progress must depend on a thorough understanding of the genetic architecture of host-parasite populations and the specific genetic interactions involved among different host genotypes and pathogenic races. Presently, our knowledge of these matters in the pine rusts is limited. Little is known about mechanisms and modes of inheritance of resistance in hosts, or even some basic aspects of the taxonomy, life cycles, and sexual behavior of the fungi.

The intrinsic difficulties of working with wild, heterozygous, and long-lived forest trees simply do not make traditional breeding methods feasible for answering some of these questions. However, promising new approaches to analyzing genetic interactions of host-parasite combinations now exist and will be discussed later in this paper.

RESISTANCE TO FUSIFORM RUST OF SOUTHERN PINES

VARIATION AMONG SPECIES AND HYBRIDS

Among the four major (and closely related) southern pines, slash (*Pinus elliottii* Engelm.) and loblolly (*P. taeda* L.) are highly susceptible, longleaf (*P. palustris* Mill.) highly resistant, and shortleaf (*P. echinata* Mill.) nearly immune to fusiform rust (caused by *Cronartium fusiforme* Hedgc. and Hunt ex Cumm.) under natural conditions (Siggers, 1955; Schmitt, 1968; Wakeley, 1969; Derr, 1966). Thus, an early and

logical approach to breeding for resistance was through hybridizing the susceptible but commercially preferred species with the resistant ones.

This approach has proved successful in numerous hybrid and backcross combinations among these species tested at the Institute of Forest Genetics, Gulfport, Mississippi, and elsewhere. Although few parents were used, trends have emerged clearly. Hybrids with shortleaf are very resistant to fusiform rust, and those with longleaf only slighly less so. Progenies from two loblolly x slash crosses, on the other hand, were much more susceptible than any other hybrid or their parental species (Henry and Bercaw, 1956; Henry and Jewell, 1963; Jewell, 1959; Derr, 1966; Schmitt, 1968).

Early reports (Jewell, 1959; Jewell and Henry, 1961) suggested that resistance was inherited from shortleaf in a simple, dominant manner. Later analyses showed that some progenies with half to one-quarter of their genes from shortleaf developed galls in varying amounts but were still relatively highly resistant. Backcross progenies between moderately susceptible Sonderegger pine (the natural longleaf x loblolly hybrid) and its resistant parent species (longleaf) were much more resistant than progenies from its susceptible parent (loblolly). On the basis of this gradient in susceptibility among hybrids, Schmitt (1968) proposed that resistance was inherited polygenically and perhaps at different loci from different species.

Artificial inoculation of hybrids with shortleaf pine also pointed to a more complex mode of inheritance. Although hybrids were generally intermediate between parent species in susceptibility, individual progeny means ranged from 4 to 92% infection, depending on the particular combination of parents used. These tests showed that the parent of the susceptible species was as influential as that of the resistant species; in other words, susceptibility appeared to be as strongly inherited as resistance (Jewell, 1961a, 1965).

RACIAL VARIATION WITHIN SPECIES

Provenance tests provided the earliest and most extensive evidence for genetic variation in susceptibility to fusiform rust. In no other trait have genetic differences among seed sources been so strongly and consistently expressed. In the Southwide Seed Source Study (Wells and Wakeley, 1966), seed lots from 15 sources throughout the geographic range of loblolly pine were tested in plantations near each source. Severity of infection varied greatly among test sites. But in those sustaining heavy infection, the range between the most and least susceptible sources was consistently on the order of 50 to 75%, and always in the same pattern: the most resistant sources were from near the extremities of the species range--west of the Mississippi River and eastern Maryland (Wells and Wakeley, 1966). With the exception of the Maryland source, resistance tended to increase with the western longitude of the seed source. These results are consistent with those of similar studies of more limited scope (Kraus, 1967; Wells, 1966; Wakeley, 1969).

A surprising degree of variation in susceptibility also exists among stands within a local region. Significant differences were found among seed sources from proximate stands in Louisiana (Crow, 1964), Texas (Wells, 1966), and Georgia (Barber, 1966; Kraus, 1967). Two of the

studies (Wells, 1966; Kraus, 1967) included seed from a few distant sources. They showed that the local variation occurred within the broader pattern of geographic variation described above.

Reasons for these patterns of variation are not known, though two hypotheses have been advanced. Wells and Wakeley (1966) proposed that varying degrees of selection pressure imposed by the rust in different parts of its host's range could have generated corresponding variation in frequencies of genes for resistance. Presumably, this hypothesis would demand that the most effective selection for resistance evolve near the gene center of the pathogen and host. They countered their own argument by pointing out that populations with the greatest resistance now exist where the incidence of the disease and conditions for it are minimal--namely, at the extremities of the species range--and that there is no evidence that the situation was ever otherwise.

The argument for selection pressure cannot be discounted on a local level, however. Since very young trees may be intrinsically more susceptible than older ones, and certainly more liable to die once infected (Siggers, 1949), and since the frequency and severity of rust epidemics fluctuate widely in different years and regions, different stands may be subjected to varying degrees of selection pressure from the pathogen within a single generation. Because individual trees within a stand vary in susceptibility, it is reasonable to conjecture that a young stand subjected to a severe epidemic would have gene frequencies quite different from those of a stand that escaped infection until relatively mature. The genetic bottleneck that second growth stands regenerated by one or few seed trees commonly go through in the South after logging or an agricultural field is abandoned could produce the same effect (Kinloch and Stonecypher, 1969).

A more plausible explanation for the geographic pattern of variation observed is introgression of shortleaf genes into loblolly (Wells and Wakeley, 1966). Evidence for this hypothesis is the known resistance shortleaf imparts to its hybrids, and the fact that where the two species overlap or exist in mixture (especially west of the Mississippi River), intermediate forms occur (Wells and Wakeley, 1966; Kinloch and Stonecypher, 1969; Zobel, 1953)--both in morphological traits and in protein profiles (Hare and Switzer, 1969).

Racial variation in resistance to rust apparently does not occur in slash pine (Snyder, Wakeley, and Wells, 1967; Gansel and Squillace, 1965).

INDIVIDUAL VARIATION

The patterns of geographic variation demonstrated are interesting from the standpoint of evolutionary changes in the genetic structure and gene frequencies in host populations. But practical utilization of variation in resistance for tree improvement will depend more on variation found among individual trees. That a large amount of such variation exists has been amply confirmed in progeny tests of both slash (Barber, 1964; La Farge and Kraus, 1967) and loblolly (Woesner, 1965; Barber, 1966; Kinloch and Stonecypher, 1969) pines.

In the most extensive of these studies (Kinloch and Stonecypher, 1969), controlled- and open-pollinated families from a large number of randomly chosen parent trees growing in a natural stand were outplanted in an area of moderate to high hazard from fusiform rust. The same families were replicated on different but proximate sites that varied considerably in their edaphic properties and in the amount of rust that subsequently developed on the trees. After a natural epidemic, family means ranged from 0.5 to 10.8 galls per tree on the site with the most rust, and from 0.0 to 2.2 on the site with the least. Estimates of heritability, on a family basis, were high (0.65 to 0.85) and remarkably consistent for both controlled- and wind-pollinated families on all sites.

This study also showed the influence of site in predisposing trees to increased susceptibility. The sevenfold range in the amount of rust observed on different sites was most strongly associated with factors in the edaphic environment, particularly the previous cultural history of the sites. Thus, trees on sites that had been forested and relatively undisturbed before planting had the least amount of rust; those on sites that had been intensively cultivated up to or within a few years of planting had the most. This evidence, though circumstantial, was consistent with independent observations of the effects of cultivation, fertilization (Gilmore and Livingston, 1958), planting on old fields (Siggers and Lindgren, 1947), and other site-disturbing treatments (Miller, in press) that increase the intensity of fusiform rust infection. These results have important and obvious implications for future plantation and second growth management which increasingly will tend to alter natural forest sites by similar cultural practices. These cultural treatments will put an even higher premium on obtaining stable genetic resistance. Fortunately, families highly resistant and susceptible to rust consistently maintained their relative rankings in susceptibility on all sites--even though the absolute amount of rust may have increased greatly from one site to another. Furthermore, relatively highly resistant families were much less affected by site influence than susceptible ones.

In summary, results of studies on fusiform rust show that ample variation in resistance exists in wild host populations and that resistance is highly heritable and apparently stable over a range of natural environments. This pattern of variation may well characterize that of other pine hosts to their endemic rusts.

ARTIFICIAL INOCULATION

Although the practical value of parent material selected for tree improvement ultimately depends on field performance of progeny under normal conditions, more rapid and uniform tests for screening progenies and for basic research presumably can be accomplished by artificial inoculation. Ideally, such tests would demand exposing host material of appropriate age and stage of development to inoculum of known genetic identity, in sufficient and standard amounts to enable prediction of progeny performance under conditions of acute hazard in the field. These requirements have yet to be fulfilled adequately.

Recurrent objections to artificial inoculation, as it has been practiced (e.g., Jewell, 1960; Kinloch and Kelman, 1965), are that overwhelming doses of inoculum applied under environmental conditions optimal for the pathogen may only screen for immunity, masking relative levels of resistance that might still be effective under field conditions.

Another objection is that young succulent seedlings in the cotyledon and primary needle stage--especially in nursery and greenhouse environments--may be intrinsically more susceptible than older ones grown naturally. The much greater infection of shortleaf x slash hybrids inoculated artificially (Jewell, 1961a,b) as opposed to naturally (Henry and Bercaw, 1956) and of juvenile compared to 1-year-old seedlings inoculated artificially (Jewell, 1960; Goddard and Arnold, 1966) suggest such a relationship. In one study that compared the amount of infection occurring on 16 open-pollinated families by both natural and artificial inoculation, a low (0.46) correlation in progeny performance was found between the two methods (Kinloch, 1968). More such comparisons are needed to evaluate the practical utility of artificial inoculation.

Nevertheless, the method has been useful in detecting genetic differences in susceptibility among progenies (Goddard and Arnold, 1966; Kinloch, 1968; Davis and Goggans, 1968), and in studies on modes of inheritance of resistance. The most intensive and reliable work has been done at the Institute of Forest Genetics, Gulfport, Mississippi (Jewell and Mallett, 1967). Inoculation of progenies from a few slash pine parents phenotypically selected for resistance or susceptibility demonstrated that certain rust-free parents consistently transmitted about 50% resistance to either open-pollinated progenies or to those from crosses with susceptible parents, and up to 90% resistance in specific combination with other resistant parents. The nearly complete susceptibility of progenies from susceptible x susceptible crosses and the segregation (1 resistant: 1 susceptible) of progenies from resistant x susceptible crosses suggested that resistance was inherited by a single dominant gene that was heterozygous in the resistant parents (Jewell, 1966). Although subsequent data were not entirely consistent with this hypothesis (Jewell and Mallett, 1967), the discontinuous distribution of progenies into groups that were either highly resistant or highly susceptible still suggested a relatively simple mode of inheritance.

RESISTANCE TO OTHER PINE STEM RUSTS

Evidence of genetic variation in host resistance to other pine stem rusts is scanty, but similar in kind to that for fusiform rust. There appear to be distinct differences in susceptibility to sweetfern rust (*C. comptoniae* Arth.) among pine species both native (Kaufman and Mains, 1915; Spaulding, 1917) and exotic (Molnar, 1961) to the natural range of the fungus. Two hybrid progenies from *P. banksiana* Lamb. x *P. contorta* Dougl. crosses differed from their parental species and each other in susceptibility to this disease and also to eastern gall rust (*C. quercuum* (Berk.) Miyabe ex Shir.)(Anderson and Anderson, 1965). Recently, highly significant differences in susceptibility to eastern gall rust were found among range-wide seed sources of jack pine planted in Wisconsin (McGrath, 1967). As with fusiform rust on loblolly pine, the relative rankings in susceptibility of the 12 sources used were fairly consistent over the 3 test plantations, though the intensity of infection in each plantation varied considerably. In Europe, a few reports have indicated similar variation in susceptibility to *Peridermium pini* (Pers.) Lév. among different seed sources of Scots pine (*P. sylvestris* L.) and also among individual parent trees (van der Kamp, 1968; Klingström, 1967).

Great variation in susceptibility to the western gall rust (*Peridermium harknessii* Moore) is common among individual trees in natural stands of native pines and planted Scots pine. Trees with hundreds to thousands of

rust galls exist in proximity and otherwise similar conditions to those with none (Peterson, 1960; York, 1929). That such striking differences are genetically determined is probable, but has not yet been clearly demonstrated. Results of inoculation of ponderosa pine progenies from heavily infected and rust-free parents growing at the Institute of Forest Genetics, Placerville, California, have been inconclusive (unpublished data). Although no parent tested was found to transmit a high degree of resistance to its offspring, marked variation among individual trees was found in the type and rate of symptom development. Several trees withstood repeated inoculation (Quick, 1966). These results were very similar to those of Hutchinson (1935) and True (1938), who made numerous field inoculations of planted Scots pine in New York.

MECHANISMS OF RESISTANCE

Siggers (1955) proposed that differences in the phenological development of trees might be causally associated with corresponding differences in susceptibility to fusiform rust. He reasoned that trees that broke winter dormancy earlier would be more in phase with the seasonal development of the pathogen and would expose succulent, susceptible new shoots to the basidiospore stage for a longer period of time. The greater susceptibility of trees that had been cultivated and fertilized (Gilmore and Livingston, 1958), planted on old fields (with presumably high residual fertility) (Siggers and Lindgren, 1947), or exposed to fire was attributed to an induced early break in dormancy. No definitive evidence to support this hypothesis has been advanced, however, and it can be argued equally plausibly that shoots that develop sooner also harden off sooner and become more resistant. True (1938) found that resistance in Scots pine to the so-called Woodgate rust (*P. harknessii*) increased with age of shoots during a single season. He observed that aeciospore germ tubes penetrated the cuticle and epidermis of resistant and susceptible hosts alike, but only in less lignified portions of the shoot before periderm formation. It seems likely that most pathogens that have shoots (as opposed to needles) as their primary infection courts would meet with the kind of functional, ontogenetic resistance described. The critical questions are how strongly variation in seasonal phenology or rate of maturation are inherited, and whether they are genetically correlated with varying degreees of susceptibility. In jack pine, at least, the evidence is negative--seed sources that differed in susceptibility to eastern gall rust all broke dormancy at about the same time (McGrath, 1967).

Experience with crop diseases, especially rusts, has taught that resistance is more often a dynamic process of host response to a pathogen on a protoplasmic level than a static precondition of the host. Hutchinson (1935) and True (1938) identified three general types of host response following field inoculation of phenotypically resistant and susceptible trees of Scots pine with *P. harknessii*: (a) typical gall formation of susceptible hosts; (b) atypical, often abortive gall formation of partially resistant hosts, characterized by cracked, resinous bark; and (c) small necrotic spots, occasionally followed by slight swellings that failed to develop further, on resistant hosts. Although Scots pine is not a natural host of *P. harknessii*, similar symptoms found on ponderosa and other native pines (York, 1938; Quick, 1966) suggest that these responses were characteristic.

The degree of compatibility between host and parasite was measured by the type and rate of symptom development (Hutchinson, 1935; True, 1938). In the most compatible reactions, incipient swellings were the first macroscopic symptom discernible. In the most resistant reactions, spots with well defined margins and necrotic, tannin-filled epidermal and subjacent cells developed within 6 weeks. Spots with diffuse margins that appeared water soaked usually indicated successful infections, especially when their appearance was delayed. In partially resistant hosts, hypertrophic and hyperplastic reactions of affected tissues impeded intercellular spread of mycelium by mechanically restricting available growing space. Formation of wound periderm, often in successive layers, also resisted spread, but was completely successful only when invaded contiguous cells died rapidly. All invaded cortical cells eventually died, and normal gall formation ensued only if and when mycelium could reach the cambium. Thus, the rate of response of host cells to the biochemical and mechanical lesion imposed by the parasite determined the degree of resistance. This condition appears no different in kind to hypersensitive mechanisms of resistance in many other host-parasite combinations.

VARIATION WITHIN RUST POPULATIONS

The taxonomic history of *Cronartium* and its imperfect stage, *Peridermium*, has been very confused, with many synonymous and invalidly named species. Peterson (1967) recently brought considerable order to the genus in his treatment of the aecial (*Peridermium*) stages on pines, but pointed to serious remaining gaps. Some of the named species, such as *C. flaccidum* (Alb. & Schw.) Wint. (including *P. pini*) and *C. coleosporioides* Arth. (including *P. stalactiforme* Arth. & Kern, *P. filamentosum* Peck, and *P. harknessii*) are quite difficult and exist in complexes of subspecific or racial varients; these vary in their alternate host preference or lack alternate hosts entirely. Further work may eventually elevate some of them to specific status. Obviously, a clearer definition of the various taxa is needed before host affinities can be firmly established and definitive genetic studies started.

Within species, racial variation has been demonstrated for albinism in *C. fusiforme* (Kais and Walkinshaw, 1964), *P. stalactiforme* (Powell, 1966), and *P. harknessii* (Mielke and Peterson, 1967); for phenology, spore morphology, and conditions for germination in *P. filamentosum* (Peterson, 1968); and for germ tube growth, life cycle, and nuclear behavior in *P. pini* (Hiratsuka, 1968) and *P. filamentosum* (Christensen, 1968, 1969).

On the all important question of variation in pathogenicity on pines, little is known. Klingström (1967) reported variation in virulence in 3 aeciospore sources of *P. pini*. One source was avirulent on Scots pine progenies used in his experiments, but not on other material. True (1938) lacked proof, but interpreted the variation in symptoms he observed on Scots pine trees inoculated with *P. harknessii* to be indicative of variation in virulence among individual spores. In loblolly pine, the maintenance of the same relative rankings in susceptibility of different seed sources planted throughout the southern U.S.A. was taken as negative evidence for the existence of pathogenic races of *C. fusiforme* (Henry, 1959). Snow, Powers, and Kais (1969), however, found distinct variation in pathogenicity among isolates from different areas on open-pollinated seedlings of a single slash pine parent.

By analogy with other rusts, variation in pathogenicity is to be expected, though much more work is needed to determine its extent in present populations of pine rusts and the inherent capacity for change in these populations. The amount of variation in pathogenicity bears critically on the degree of stability of resistance that can be expected in pine populations following selection.

The potential for change to races of wider virulence depends in large part on the types of sexual behavior and other mechanisms of gene exchange operating in rust populations. If virulence is controlled by several different major genes as, for instance, in gene-for-gene systems, a homothallic sexual mechanism presumably would impose some restriction on the range of variability possible and the capacity of the population to synthesize new gene combinations for virulence. Although critical evidence is lacking, present indications are on the side of limited gene exchange in the pine rusts as compared, for example, with the obligately outcrossing wheat stem rust. Hirt (1964) found that cross-fertilization by pycnial exchange was not prerequisite to aeciospore formation in *C. ribicola*, suggesting that homothallism is at least possible, if not predominant, in this fungus.

In the autoecious species (*P. harknessii*, races of *P. pini*, and probably *P. filamentosum*), a sexual stage is either lacking altogether or is highly irregular. Hiratsuka, Morf, and Powell (1966) proposed an endo-type life cycle for *P. harknessii*. Their conclusions were based primarily on the number of nuclei observed at various stages of aeciospore maturation and germination: immature aeciospores had 2 nuclei, mature aeciospores 1, and germ tubes 1 in each of 2 to 4 septate cells formed. Aeciospores of *P. stalactiforme*, by contrast (and typical of host-alternating species) remained dicaryotic throughout and lacked septate germ tubes. They interpreted the sequence observed in *P. harknessii* as indicating nuclear fusion in mature aeciospores followed by meiosis and monocaryotization of germ tube cells. A similar sequence was found in pine-to-pine races of *P. pini* and interpreted in the same way (Hiratsuka, 1968).

Evidence of other workers, however, differs in considerable detail, and leaves this conclusion far from definite. True (1938) and Christenson (1968) found that most aeciospores of *P. harknessii* were dicaryotic, and saw no evidence of nuclear fusion. In a later paper, Christenson (1969) observed that dicaryotic aeciospores of an albino race became uninucleate during maturation, but that subsequent division of nuclei was more characteristic of mitosis than of meiosis. In autoecious races of *P. filamentosum*, nuclear number is extremely variable, ranging from 1 to 6 in aeciospores and up to 16 in their germ tubes (Christenson, 1968). Only 15% of germ tubes became monocaryotic (Krebill, R. G., manuscript in preparation). From these inconsistencies, the question of a sexual stage in autoecious peridermia remains unresolved. The only conclusion warranted presently is that nuclear number and behavior in these species are highly unstable. In any case, mechanisms of gene exchange within the populations appear to be limited.

NEW APPROACHES TO ANALYSIS OF GENETIC INTERACTIONS IN WILD HOST-PATHOGEN POPULATIONS

Development of the gene-for-gene hypothesis has provided both a penetrating insight into the genetic structure and evolutionary mechanisms of host-parasite relationships and a powerful tool for applied research. Person (1959, 1966, 1967) discussed the origin of complementary genes as an effective strategy for enabling both host and parasite to survive under the mutually antagonistic selection pressures imposed by each. Mode (1958) showed by a mathematical model how these genes would soon reach equilibrium at intermediate frequencies in wild, outcrossing populations as a necessary condition for their coevolution. Further elaboration of the theory and evidence for it are discussed elsewhere (Flor, 1955; Mode, 1958; Person, 1959). The usefulness of the theory derives from the kinds of predictable properties intrinsic to complementary genic relationships. These properties were described by Person (1959) who showed how their recognition in any specific host-pathogen system *ipso facto* implied the existence of such a relationship, and also could form the basis of a complete genetic analysis of the system.

An elegant example of the efficacy of Person's analytical approach was demonstrated by Noronha-Wagner and Bettencourt (1967), who studied leaf rust of coffee, caused by *Hemileia vastatrix* Berk. & Br. This is a difficult system and in several ways analagous to the autoecious *Peridermia* on pines. Both hosts are long-lived trees with high degrees of heterozygosity. The life cycle and sexual behavior of *H. vastatrix* is as unconventional and obscure as some of the peridermia. Nevertheless, in only one generation of breeding, they were able to identify four dominant genes for resistance in the host population, infer their complements for virulence in the pathogen, and predict the likely existence of four other pathogenic races not yet isolated in nature.

The method depended on characterizing the reaction spectrum elicited by each of 12 physiological races of the rust on each of a set of 8 host clones that differentiated them. Progenies obtained by selfing the various clones were usually either identical to their parents in reaction to the 12 races, which indicated that parents were homozygous at loci for rust reaction, or segregated into parent-type reaction and susceptibility to all races in a 3:1 ratio, implicating a dominant gene in the heterozygous condition in the parent. Occasionally, selfed offspring segregated into three reaction categories which included, in addition to parental type and susceptibility to all races, a third reaction type characteristic of another host differential. This second kind of segregation pattern suggested heterozygosity at more than one locus in the parent. Subsequently, various F_1 crosses among selected differentials produced an array of genotypes with all possible combinations of the four genes (Table 1) and confirmed their identity and dominance relationships.

Elements for the genetic analysis of this host-parasite combination thus consisted only of a variable rust population, a variable host population (both subject to cloning), and the selfed and F_1 generation of the latter. Recognition of the properties that inhere in a gene-for-gene system enabled elucidation of the relationship and number of complementary genes involved. The key property is the complementary geometrical series of host-pathogen interactions, in which, for each additional gene for resistance in the host, the number of races capable of attacking it is reduced by half (Table 1). With host genotypes falling into this kind of array, corresponding and complementary genotypes of the pathogen were deduced as a logical and necessary consequence of the theory.

Table 1. Genetic interactions of coffee and its leaf rust. S indicates susceptible, blanks resistant. (Adapted from Noronha-Wagner and Betterncourt, 1968, and Person, 1959)

| Race designation | Rust genes for virulence | Host Differentials: Host Genes for Resistance | | |

This type of approach seems well adapted to studying rust diseases of pines, especially the autoecious peridermia. Isogenic (or nearly so) aecial clones could be obtained in quantity from single spore inoculations (or perhaps even single gall isolates), tested on different host clones to determine reaction spectra, and then on selfed and F_1 progenies to determine modes of inheritance, in the manner just described.

With heteroecious species of *Cronartium*, the technical problems are more difficult, especially in securing genetically homogeneous inoculum. Since the basidiospore stage that infects pine is a product of meiosis, each spore is potentially a different genotype. Relative uniformity could be obtained by establishing clones derived from single aeciospore or urediospore inoculations on alternate hosts. Complete homozygosity in different isolates would be assured in both haplophase and dicaryophase if the fungus in question were homothallic, as Hirt (1964) has suggested for *C. ribicola*.

In the context of this discussion, I would now like to return to experience of my own with fusiform rust, described earlier in this paper and in Kinloch and Stonecypher (1969). This was a population study of open- and controlled-pollinated offspring derived from a large number of randomly selected parent trees and planted on different sites. Early plantings sustained negligible rust infection for several years. But after an epidemic in 1964, infection was widespread in all plantations, though the intensity varied greatly among sites and families. I have already mentioned the high heritabilities of resistance obtained. While characterizing a population by quantitative parameters is valid and helpful for utilitarian purposes, it is not likely to lead to an understanding of the biological mechanisms involved. Another approach to the same raw data is possible, which may provide a deeper insight to the genetic structure of the host-pathogen population and point to alternative routes of investigation.

When individual trees on a given site, irrespective of family relationship, were grouped into successive categories according to the number of separate infections (galls) they had, their frequency distribution appeared as in Fig. 1, A and B. Similar data were obtained in another sample of trees from bulk seed lots of unknown parentage (Fig. 1C). The latter were in a different experiment at a distant site, but were approximately the same age and infected in the same year as the former. The close resemblance of these sample distributions suggests that they characterize the response of a young population following exposure to relatively heavy infection. Individual families, on the other hand, had distributions peculiar to each. Fig. 2 illustrates the frequency distributions of individual trees within the same full-sib families representative of high, intermediate, and low susceptibility on each of three sites that differed greatly in the amount of over-all infection.

It is clear from the overall distribution of the sample populations (Fig. 1), as well as the differences in the distributions among full-sib families (Fig. 2), that a wealth of genetic resistance exists in the population. It is also apparent that different degrees of resistance exist, and that most individual trees have some--even in relatively susceptible families. In these tests (and commonly in natural stands), individual trees with more than 10 and up to 50 galls were often adjacent to those with few or none. Most families included individuals with more than four times the number of galls as the mean for that family (though individual extremes in resistant families always had fewer galls

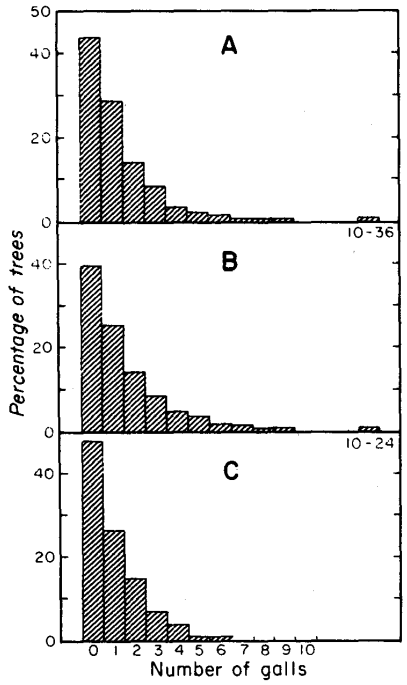


Figure 1.--Frequency distribution of individual loblolly pines into categories according to the number of separate infections (galls) sustained by each. (A) 7-year-old trees (total: 3,918) from 48 open-pollinated families; (B) 4-year-old trees (total: 1,376) from 54 controlled-pollinated families; (C) 4-year-old trees (total: 318) from bulk seedlot, unknown parentage. (Data for C courtesty of the U.S. Forest Service, Macon, Ga.)

than their counterparts in susceptible families--see Fig. 2). Since these extremely susceptible individuals were randomly distributed geographically, the assumption of approximately equal and abundant distribution of spores over the test sites seems valid.

It then seems intuitively evident that the variation in number of galls on individual trees is inversely related to the number of genes for resistance the trees inherited. An interesting and perhaps significant feature of the test populations is that the distribution patterns of trees into "gall categories" appear to fall into a geometrical series, wherein the number of trees in each succeeding category is roughly half of the preceding one, up to 5 or 6 categories (Fig. 1). As already discussed, geometrical series are properties of gene-for-gene relationships (cf. Table 1 and Person, 1959). The same kind of series theoretically would be expected in the coffee-leaf rust system if host genotypes were simultaneously inoculated with an equal mixture of each pathogenic race: the number of pustules counted per leaf should decrease by multiples of one-half as the number of genes for resistance in individual plants increased from 0 to 4.

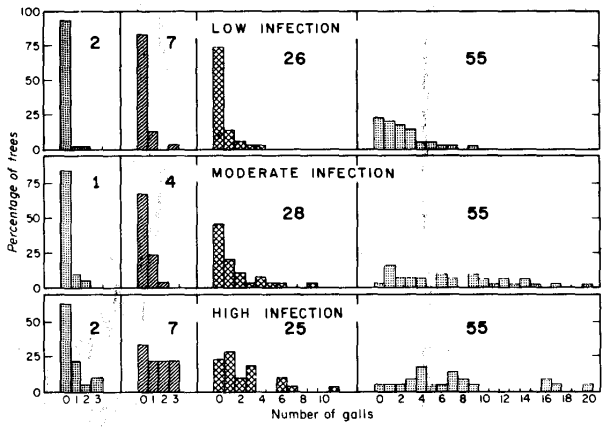


Figure 2.--Frequency distribution of individual trees in four full-sib families of loblolly pine into categories according to the number of separate infections (galls) sustained by each. The same four families (of a total of 55) were planted on each of three different sites that had relatively low, moderate, and high levels of rust infection. Numbers in bold face are the relative ranking in resistance of the same family on each site.

From this kind of relationship it is tempting to speculate that the number of loci controlling resistance and susceptibility could be roughly inferred from the number of discrete categories detectable in the series. The assumptions required, however, are numerous, and any conclusions of this kind drawn from such crude data would be premature and extremely teneous. The data do provide, on the other hand, a clue to the kinds of genetic interactions that may be occurring in the population. The distribution patterns of individual trees in the population as a whole, as well as individual families within, are suggestive of a heterozygous parent population segregating at several major polymorphic loci conditioning resistance and susceptibility, similar to theoretical models of host-parasite realtionships in wild populations proposed by Mode (1958) and Person (1959, 1966, 1967). I submit this as a working hypothesis that is testable by the approaches discussed.

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FLOOR DISCUSSION

(Discussion here also covers the previous paper by Patton.)

ZUFA: I have a question for Dr. Patton. How fast does the blister rust mycelium grow through the needle? How soon after the inoculation can it reach the stem?

PATTON: I think Hirt has reported that the minimum time required was about 11-1/2 hours or so. A number of experiments, that were done by Dr. Riker in the early days indicated a minimum time of about 18 hours. So I would say 12 to 18 hours might well be the minimum. This is from the time that teliospores start to germinate, and basidiospores are cast, germinate, and penetrate. I don't know anything at all about the time required for the actual penetration process, but I don't suppose this really takes too long. We have seen vesicles in needles with infection hyphae well down into the mesophyll within 5 days after the inoculation period was started. We gave needles about a 60 or 72 hour inoculation period, and then made our first collection some 5 days after the beginning of inoculation. By that time, the hyphae was well down into the needle; mycelium had started to form, in other words.

BEGA: I have three questions for Dr. Patton. First, a comment, though. Thank you for reiterating this need for some more basic problem oriented studies on *Cronartium ribicola*, and I hope that you and our friend Leaphart here can keep your groups working in the direction you are. The first question is, have you observed on secondary or tertiary sporidia the percent of vesicle formation either on needles or on cellodian membranes?

PATTON: We made no counts of that at all.

BEGA: It's unimportant. I was just curious. The other had to do with needle age in relation to infection. We aged cankers using the Lachmund method for western white pine or Kimmey method for sugar pine, which are both the same, but we count the second-year needles, as infection counts. I think your work is going to throw some light on some of the variables that we have been coming up with relating canker age to climatic years. And then, third, what is the role of the stomata in these older needles that are plugged?

PATTON: Well, as I said, this is one of these things that we still don't have all the answers to yet. I think that the stomatal plugs play a primary role in the difference in amount of infection we get from the primary and secondary needles. I don't mean to say that primary needles aren't plugged, because they do have plugs, but I think that the number of chances for germ tube entry down as far as the guard cells are much greater in primary needles than in secondary needles. Now, what I'd like to do is follow this thing through. I have the feeling or the impression, and some of our data tend to support the idea, that there is greater plugging as the needle gets older, and perhaps even with some of our

resistant selections. I think our number 327, for instance, has very heavily plugged needles. I have the impression that as the trees get older, there seems to be a tendency for greater wax production, and greater plugging, but there are still enough chances and enough openings available for germ tubes to get in, and somehow or other, they seem to find these openings. I don't think I have ever seen any evidence, however, that a germ tube can bore its way down through one of these solid plugs. I am pretty well convinced it cannot do that, but apparently there are enough cracks and crevices and openings so it can get by. Also, in looking at this aspect with the scanning electron microscope, and we did this for the first time last week, our view was confirmed, but we'd like to know more. The plugs don't look as thick and as impenetrable as we first thought, although I think as the plugs get very old a heavy, plate-like covering forms on a good many of these.

VIDAKOVIC: I studied the needle structure of European black pine (*P. nigra*) and I found that there is a great variation on the wax formation within the different subspecies of this species, and also it seems to me that there is a positive relation of wax formation within 1-year-old needles and 2-year-old needles. Very definitely I think that, on 2-year-old needles, plugs are usually the case and the spores can grow in.

PATTON: You tend to confirm the findings that we have come up with? Thank you.

PHYSIOLOGY AND BIOCHEMISTRY OF RESISTANCE TO PINE RUSTS

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ABSTRACT

This paper reviews the literature on physiology of tree-rust resistance, mostly that to *Cronartium* rusts on North American pines. The principal resistance mechanisms against white pine blister rust are hypersensitivity of foliage and stem cells, and production of periderm barriers in the stem in response to infection. After blister rust infection, phenolics appear to increase more in resistant than in susceptible pines. Resistance in southern pines to fusiform rust may be more passive (preformed); hypersensitive reactions and periderm barriers seem much less important with this disease than with white pine blister rust. But resistance to fusiform rust is physiological since hypodermic injections do not bypass resistance mechanisms and resistant species show transient infection symptoms.

Although fusiform rust infection does not stimulate height growth, it increases both auxin and gibberellin content as well as IAA oxidase and PPO activity in pine seedlings. In a resistant species, these effects are transient, coincident with infection symptoms. Thus, resistance is not due to lack of growth substances for gall development. A positive correlation between resistance and PPO activity suggests a quinone resistance mechanism. Evidence is presented for both phytoalexin and preformed fungitoxin production correlated with fusiform rust resistance. Basidiospore germination and germ-tube growth are frequently inhibited by diffusates and extracts from uninfected resistant tissue and promoted by similar preparations from susceptible tissue.

Fusiform rust resistance in loblolly pine is apparently associated with peculiarities in terpene composition and electrophoretic protein patterns. Protein and morphological similarities suggest introgression with shortleaf pine as a source of loblolly resistance. Certain isozyme patterns of a number of enzymes are associated with rust resistance and may serve as markers in breeding for resistance.

Although *Cronartium*, *Peridermium*, and *Melampsora* fungi cause rusts on numerous tree hosts, by far the greatest economic loss is to *Cronartium* rusts on pine. Most of the literature reviewed here concerns the two most important, white pine blister rust, caused by *C. ribicola* J. C. Fisch. ex Rabenh., and southern fusiform rust, caused by *C. fusiforme* Hedgc. & Hunt ex Cumm. Included in this review is a summary of my work with *C. fusiforme* at Gulfport, Mississippi, and the University of Florida. The primary goal of my research was to identify resistance mechanisms that might be exploited to develop resistant trees.

GENERAL PHYSIOLOGICAL MECHANISMS OF RESISTANCE

HYPERSENSITIVITY

Although morphological barriers may also be significant, foliar resistance to tree rusts appears to be primarily physiological, like most resistance mechanisms in plants (Rubin and Artsikovskaya, 1963). Fusiform rust seems able to infect pines only through cotyledons, primary needles, and stems of seedlings, and through the succulent stems of older plants. Hardened stem tissue and even young secondary needles seem immune (Jewell, 1960). When he injected basidiospores into slash pines (*Pinus elliottii* Engelm. var. *elliottii*), Powers (1968) found that infections too far out on the cotyledon did not reach the stem before the cotyledon was shed. He suggested that secondary needles may be susceptible, but that the hard needle-bundle sheath prevents close infection and that rapid growth of young infected needles may not allow the mycelium to reach the stem. I have failed to produce infection symptoms by injecting basidiospores close to the base of very young and older secondary slash pine needles or into hardened stems. Injection of the same material into susceptible tissue caused galling in nearly 100 percent of the trials (Hare, 1970). I have obtained similar negative results with shortleaf pine (*P. echinata* Mill.) seedlings. Therefore, resistance in secondary needles and hardened stems of susceptible pines, and in seedlings of a resistant species, involves physiological or biochemical factors in addition to possible external morphological barriers to penetration.

In resistant shortleaf pine, injection (Hare, 1970) or external inoculation (Jewell, 1966)of seedlings frequently induces needle symptoms and even temporary stem swelling, but a sporulating gall is not produced with *C. fusiforme*. Presumably, the incipient infection is repulsed by some physiological or biochemical means.

Although hypodermic injection does not usually bypass resistance mechanisms, there may be exceptions. Western sources of loblolly pine (*P. taeda* L.),which are more resistant than eastern sources in the field (Wells and Wakeley, 1966), all produced galls when injected in the epicotyl (Hare, 1970). Galls frequently showed up later and developed slower in western than in eastern sources, however. When outplanted, more of the inoculated western sources were severely stunted and killed during the first year in what may have been a massive hypersensitive reaction to fungus injection. Water-injected controls grew normally.

According to Pierson and Buchanan (1938), current-season needles of western white pine (*P. monticola* Dougl.) are more resistant to blister rust than older needles. With eastern white pine (*P. strobus* L.), seedling resistance increases with age (Patton, 1961; Van Arsdel, 1968) and secondary needles are susceptible. Resistance of Scots pine (*P.*

sylvestris L.) to *C. flaccidum* (A. & S.) Wint.is greatest in small seedlings and mature trees and least in developing trees (Björkman, 1966). Foliar resistance to blister rust is important in western white pine, on which it may prevent stem invasion from the needles (Hoff, 1966). Similar effects have been noted for resistant slash pine seedlings inoculated with fusiform rust (Jewell and Mallett, 1967).

Alternate hosts also have foliar resistance which appears to be physiological, at least in young leaves (Anderson, 1939). Only young, soft water oak (*Quercus nigra* L.) leaves are susceptible to *C. fusiforme* aeciospores or uredospores which produce uredia in very young leaves and telia in slightly older leaves (Snow and Roncadori, 1965). But soft leaves of some water oak seedlings show only a hypersensitive flecking in response to infection (Eleuterius, 1968). Dwinell (1969) reported a similar hypersensitivity of black oak (*Q. velutina* Lam.) to *C. fusiforme* but not to *C. quercuum* (Berk.) Miyabe ex Shirai.

WOUND PERIDERM BARRIERS

Bark resistance to blister rust may involve both hypersensitivity and "corking out," the formation of a wound periderm in response to infection. The hypersensitive reaction has been reported on *P. monticola* (Bingham, Squillace, and Wright, 1960), *P. peuce* Griseb. (Boyer, 1962), and *P. armandii* Franchet (Hoff, 1966). Cortical cells are killed, stopping the fungus and causing a sunken area at the base of infected needles. Patton (1966) observed hybrids which responded similarly unless the needle was killed before the fungus reached the stem. Inheritance of bark resistance is independent of that of foliar resistance, indicating polygenic control (Hoff, 1966).

Corking out was first reported as a response of *P. sylvestris* to a *Peridermium* gall rust (Hutchinson, 1935; True, 1938), but resistance was ascribed mainly to hypersensitive accumulation of tannins. McKenzie (1942) reported that resistant northern pines formed similar cork barriers and accumulated tannin in response to a *Peridermium* infection. The resistance mechanism was similar to that of wound healing. This form of bark resistance has since been described for blister rust in *P. strobus* (Struckmeyer and Riker, 1951; Boyer, 1966). In loblolly pine, fusiform rust may induce formation of perderm immediately ahead of the advancing hyphae, but in this species the barrier can do no more than retard the growth of the fungus (Jackson and Parker, 1958).

OTHER PHYSIOLOGICAL MECHANISMS

In addition to hypersensitivity and corking out, physiological resistance can involve selective toxins of host or pathogen origin, lack of an essential nutrient for the parasite, enzyme activity or inhibition, inhibition of spore germination or germ-tube growth by preformed fungitoxins, failure of the host to produce a gall or other symptoms, phytoalexin production (related to hypersensitivity), or differences in water content or mineral uptake of host tissue (Schreiner, 1966). Growth-habit resistance occurs in *P. griffithii* McClell. (syn. *P. wallichiana* A.B. Jacks.), which sheds needles before blister rust infections on them can reach the stem (Heimburger, 1962). Active resistance induced by the invader seems much more prevalent in plants than preformed or passive resistance (Allen, 1959).

GROWTH SUBSTANCES AND AUXIN CATABOLISM

Boyer (1966, 1967) has shown that indoleacetic acid (IAA) induces galls in infected white pines similar to those caused by blister rust. Since both IAA and blister rust induce hypertrophy and hyperplasia and formation of periderm, an increase in auxin may be a cause of galling. Benzimidazole and gibberellic acid (GA_3), together with IAA, further promoted formation of wound periderm similar to that in resistant seedlings. These results suggest that auxins, gibberellins, and cytokinins are involved in gall development and resistance.

Susceptibility to obligate parasites such as rusts appears to be positively correlated with vigor of the host, whereas facultative parasites tend to attack the weaker individuals (Heimburger, 1962). Illy (1966), for example, found a positive correlation between susceptibility of *Pinus pinaster* Ait. to the pine twist rust (caused by *Melampsora pinitorqua* Rostr.) and 16 measures of vigor on six parent trees and their progeny. Workers at Gulfport have noted that fusiform rust-infected nursery seedlings are frequently taller and more vigorous than their healthy counterparts. If true, this observation suggests that rust infection promotes height growth or that taller seedlings are more susceptible.

To determine whether fusiform rust promotes height growth, increases auxin and gibberellin production, or attenuates auxin catabolism, several greenhouse experiments were carried out with slash and shortleaf pine seedlings (Hare, 1970). A basidiospore suspension was injected into the epicotyls of seedlings with a fine hypodermic needle; water was injected into controls. Heights were measured monthly when samples of stems, including the injection point, were analyzed for auxins, gibberellins, and activity of indoleacetic acid oxidase (IAAO), IAAO inhibitor, and polyphenol oxidase (PPO).

Of 360 slash pine seedlings inoculated, 92% developed needle symptoms and galls. None of the shortleaf developed galls but many showed needle spots and stem swellings that lasted up to 3 months.

One would expect susceptible seedlings to need auxin for gall growth and gibberellin for enhanced height growth (if any). Resistance, then, might conceivably take the form of failure to respond to infection by producing these growth substances, perhaps through gene repression, so that galls would not develop. Although rust infection did not promote height growth during the 6-month study, it consistently (five experiments) increased the auxin and gibberellin contents of both susceptible slash and resistant shortleaf seedlings, especially during the first 2 months of infection. Three zones of auxin activity and three or four of gibberellin were located on chromatograms. One auxin was identified colorimetrically and chromatographically as IAA; one gibberellin peak coincided with that of GA_3. A strong inhibitor of both auxin and gibberellin activity, probably inhibitor β or abscisic acid (Milborrow, 1967), increased with time after inoculation. Auxin in galled slash seedlings remained elevated until the end of the study, but in shortleaf it returned to normal with the disappearance of symptoms. Gibberellins remained elevated in both species for several months after inoculation. One auxin chromatographing near the front and a gibberellin at Rf 0.6 to 0.8 seemed to be associated with gall development, appearing in older galled slash but rarely in healthy slash or in shortleaf.

These data indicate that fusiform rust resistance in shortleaf pine is not a matter of growth substances being limiting for gall development, since infection stimulated auxin and gibberellin production equally in both species.

The infection-enhanced auxin levels found in these experiments might result either from accelerated auxin production, or from greater auxin stability because of an accumulation of polyphenolic IAAO inhibitors (Hare, 1964). Assuming auxin catabolism to be suppressed, activities of both IAAO (see Lipetz, 1959) and PPO, which spares IAAO from inhibitors, should be attenuated. Instead, in 15 trials, inoculation consistently increased the activity of IAAO and PPO and decreased IAAO inhibitor content in both species for 2 to 5 months following injection. Thus, even though infection increased auxin levels, it also promoted auxin catabolism, assuming that these enzymes regulate auxin breakdown *in vivo*. Since Galston and Dalberg (1954) showed that IAAO is an inducible enzyme, the enhanced IAAO activity may also be a result of high auxin levels. Shortleaf pines consistently had higher PPO activity than slash--a possible indication that shortleaf has a resistance mechanism based on oxidation of phenols to more toxic quinones.

PHENOLS

The participation of phenolics in plant disease resistance is well known. Infection almost invariably leads to accumulation of phenolics and increased respiration due to uncoupling of oxidative phosphorylation by the phenols and enhanced PPO activity (Farkas and Kiraly, 1962; Hare, 1966). In the hypersensitive reaction, phenols of host or pathogen origin are oxidized to quinones by PPO. The quinones inactivate enzymes and kill nearby host cells, causing hypersensitive flecking. If the obligate fungus is not killed directly by the quinones, it cannot survive in the necrotic lesions. This mechanism has been well authenticated with cereal rust (Farkas and Ledingham, 1959; Kiraly, 1959; Noveroske, Williams, and Kuc, 1962; Chigrin and Aleshin, 1965).

Several studies have been made of the relation of phenols to white pine blister rust resistance. The higher tannin content in resistant periderm tissue has already been mentioned, and Offord (1940) reported more tannins in resistant *Ribes* leaves. Boyer (1964) and Boyer and Isaac (1964) found that phenols were released from eastern white pine cell vacuoles after rupture of the tonoplasts by the mycelium. The failure of tonoplasts in old cells to rupture until late in the development of the disease may account for the lower resistance of old needles. Among more than 50 phenols examined, Hanover and Hoff (1966) found no qualitative differences that could be related to western white pine resistance, but one phenol seemed more abundant in resistant trees. Hoff (1968) found that oxidation of pine extracts with peroxide, as might occur *in vivo* with PPO, increased their fungitoxicity.

PHYTOALEXINS

Phytoalexins are antibiotic substances produced by the host in response to infection (Cruickshank, 1963a,b). Resistance is dependent upon the host's ability to form phytoalexins above the tolerance level of the fungus. Other workers have not reported phytoalexin production in pine in response to rust infection.

To see if phytoalexins might be involved in shortleaf pine resistance to fusiform rust, Hare (1970) planted three 6-inch pots of soil thickly with seeds of shortleaf pine and three with slash, to form "lawns" of seedlings. After seedcoats were shed, the seedlings in the first pot of each species were misted with distilled water, those in the second pot were misted with a water suspension of basidiospores, and those in the third were misted with water, then covered with telia-bearing oak leaves. All were then incubated over water in closed jars at 20°C for 72 hours. The water droplets were blotted off the seedlings with filter paper and the paper was eluted with water and organic solvents. The combined washings were filtered and concentrated at 40°C. The aqueous residue was tested at concentrations of 0.1, 1.0, and 10.0 percent in 0.5 percent water agar against basidiospore germination and germ-tube growth. The agar was buffered to induce direct germination. Control plates contained agar made up with water or the filtrate from a spore suspension not placed on foliage. Each test was replicated three times.

Pine diffusates from seedlings sprayed with a basidiospore suspension were not as active as those from seedlings inoculated directly by spores as they were abjected from telia. The control filtrate from a spore suspension not placed on foliage had little effect, even at a 10 percent concentration. Growth of germ tubes was usually promoted by the diffusates, up to 1,100 percent by some treatments, but spore or species effects on germ tube growth were not statistically significant at the 0.05 level. Basidiospore germination on the water-agar control averaged 90.9 percent. Table 1 shows the effect of discharged spores on the activity of diffusates from the two species, when incorporated into 0.5% water agar at three levels.

At 10 percent concentration, water diffusate from shortleaf was three times as inhibitory to spore germination as that from slash, but spore diffusate from both species inhibited germination of over 99 percent of the spores. The results from the highest concentration indicate a preformed fungitoxin that is quantitatively correlated with resistance, and production of a phytoalexin by both resistant and susceptible tissue.

Table 1. Effect of diffusates in agar on germination of basidiospores. Water agar control germination 90.9%

Concentration of diffusate	Spore diffusate		Water diffusate		Spore/water ratio	
	Slash	Shortleaf	Slash	Shortleaf	Slash	Shortleaf
%	%	%	%	%	%	%
0.1	98.5	88.0	84.5	74.5	116.1	118.1
1.0	93.4	68.6	72.9	92.1	128.1	74.5
10.0	0.8	0.2	19.7	6.2	4.1	3.2

At the two lower concentrations, the spore diffusate from slash resulted in greater germination, compared to the water-agar control, whereas that from shortleaf inhibited germination. At 1.0 percent concentration, slash spore diffusate gave 128 percent of the water diffusate germination compared to 74 percent from shortleaf. Thus, at the 1.0 percent concentration, phytoalexin production was correlated with resistance, and infection apparently induced an "anti-phytoalexin" (germination promoter) in susceptible slash pine.

In addition, many of the germ tubes in plates containing 10 percent shortleaf water or spore diffusates were very short and severely curved, forked, and otherwise malformed. Shortleaf pine may, therefore, have a resistance mechanism that inhibits penetration of leaf cells.

FUSIFORM RUST RESISTANCE IN WESTERN LOBLOLLY PINE

INTROGRESSION

Western seed sources of loblolly pine have repeatedly been shown to be more resistant to fusiform rust than sources east of the Mississippi River (Wells, 1966; Wells and Wakely, 1966). Since loblolly-shortleaf hybrids are resistant (Henry and Bercaw, 1956; Henry and Jewell, 1963), and natural loblolly-shortleaf hybrids occur in Texas (Zobel, 1953), it has been proposed that resistance of western loblolly arises from introgression with shortleaf (Wells and Wakeley, 1966). Hare and Switzer (1969) showed similarities in electrophoretic patterns of seed proteins between shortleaf and western loblolly, compared to eastern loblolly. They also found morphological characteristics in western loblolly intermediate between shortleaf and eastern loblolly. The results strongly suggest introgression in the western part of the loblolly range. Fusiform rust resistance of western loblolly pine may arise from such introgression.

TERPENES

A gas chromatographic analysis of terpenes in the stem oleoresin of loblolly pines from eastern and western seed sources also turned up differences associated with fusiform rust resistance (Hare, 1970). Samples were collected in August and October from canker-free trees growing in the Harrison Experimental Forest near Gulfport. The more resistant western seed sources were compared with the less resistant eastern sources. No differences associated with resistance were found in α-pinene, camphene, myrcene, or β-phellandrene. But, at both times of sampling, β-pinene and limonene were much higher in the western than in the eastern sources. Whether these differences will prove to be a genetic marker for resistance remains to be shown.

NUTRITIONAL FACTORS

According to the nutrition theory of resistance (Garber, 1961), parasites may lose virulence because the host provides inadequate amounts of an essential nutrient at the infection site, or because nutrient uptake is inhibited by other compounds. Burrows (1960) used a leaf-sandwich technique to show that infection could pass through resistant wheat-leaf mesophyll without infecting it and infect attached susceptible leaf mesophyll. In that case, resistance was not nutritional, since nutrients could diffuse freely, but was due to an inhibitor induced by the fungus.

Chiba (1966) reported a negative correlation between the sucrose: reducing sugar ratio and resistance of poplar to *Melampsora laricipopulina* Kleb. Supplying 5 percent sucrose seemed to increase susceptibility. In addition to being a C source for fungi, sugars may complex with phenols to form more stable glycosides; high N may increase complexing of proteins with phenols. In both cases, resistance would be lowered by inhibiting quinone formation. High N content has been frequently associated with decreased resistance, while high K increases it. Trolldenier (1969) has reviewed the literature on cereal rust resistance and mineral nutrition. The N:K ratio is most important. Increasing K along with N frequently increases both yield and rust resistance. Excess N may increase the pathogen's supply of substrate in the form of amino acids and soluble carbohydrates. K deficiency tends to have the same effect. It increases the activity of hydrolases and restricts phosphorylation, causing amino acids and soluble carbohydrates to accumulate. High K promotes synthesis of insoluble carbohydrates and proteins, reducing the substrate pool for pathogens and increasing mechanical resistance to penetration.

In a field study with fusiform rust, N fertilization and cultivation quadrupled the number of cankers (Boggess and Stahelin, 1948), but the effect was probably indirect through stimulated production of rust-susceptible tissue when production of basidiospores was highest. Hutchinson (1935) and Hanover (1963) reported higher K levels in rust-resistant pine tissues. Fertilization with N decreased resistance of a poplar clone resistant to *Melampsora* rust and increased susceptibility of a susceptible clone (Donaubauer, 1966). Since NPK had no effect, N fertilization may have reduced K content of the leaves. In wheat, rust susceptibility seems to be associated with a high amino-N content or with a low C:N ratio (Barrett and McLaughlin, 1954). In general, NH_4NO_3 promotes susceptibility much more than KNO_3, and K fertilization alone promotes resistance (Trolldenier, 1969).

HOST EFFECT ON PATHOGEN

EFFECT OF DIFFUSATES AND EXTRACTS ON SPORE GERMINATION

Fusiform rust basidiospores placed on distilled water agar with a pH of about 6 germinate indirectly, forming daughter spores (secondary, tertiary, etc.) instead of germ tubes (Kais, 1963). However on water at pH 6 they germinate directly, forming long germ tubes. This "agar effect" can be reversed by buffering to pH 5 or below (Hare, 1970). Daughter spores also form on non-host tissue (Miller and Roncadori, 1966). The spores may be abjected as far as 0.3 mm. A similar response has been reported with *C. ribicola* basidiospores (Bega, 1960) which form germ tubes at pH 3 to 5, mostly daughter spores at pH 6 and above. Germination is direct on white pine needles and indirect on nonhost pine needles. Daughter spores may have survival value if they fall from resistant to susceptible tissue and then germinate directly.

Tops of 1-month-old susceptible slash pine or resistant shortleaf seedlings or both were embedded in water agar which was then seeded with basidiospores (Hare, 1970). Only those spores adjacent to the slash seedlings germinated directly, whether or not shortleaf was also adjacent. These results indicate a germination promoter diffusing from susceptible tissue, with no effective inhibition from resistant tissue. When an indicator solution was added to the agar, a yellow zone (pH 4

to 5) appeared around susceptible slash primary tissue but not around resistant slash secondary needles or shortleaf primary tissue. Susceptibility was therefore correlated with ability to lower the pH of agar by diffusion from intact tissue and induce direct germination and germ-tube growth. Water and organic solvent extracts also promoted direct germination, in this case without affecting pH. Miller (1968) found that extracts from slash and loblolly needles stimulated direct germination of *C. fusiforme* basidiospores on agar. Nighswander and Patton (1965) obtained direct germination of *C. quercuum* basidiospores on water agar by including a decoction of oak or pine foliage.

BIOCHEMISTRY OF PROMOTERS AND INHIBITORS

Anthocyanin pigments extracted from red-stemmed cold-grown slash pine seedlings which were partially resistant promoted direct germination and germ-tube growth at less than 1 ppm. They inhibited both processes at slightly higher concentrations (Hare, 1970). Water-soluble vacuole pigments were much more effective than lipid fractions and chloroplast pigments. Diffusates of intact seedlings shaken in water were more effective than aqueous homogenates, perhaps due to enzyme inactivation by phenols released from ruptured cells. High activity of acetone powder extracts and instability to heat also suggest enzyme participation.

The neutral fraction from ethyl acetate-buffer partitioning of alcoholic extracts was most active in inducing direct germination and germ-tube growth on agar. Some fractions from slash pine seedlings promoted long, thin-walled germ tubes; the same fractions from shortleaf either gave no germination or germ tubes were thick-walled, branched, and septate (cf. Patton and Nicholls, 1966). While there were great differences in the effects of various extract fractions, correlation with resistance was lower than with water diffusates from intact tissues.

PROTEIN AND ISOZYME PATTERNS ASSOCIATED WITH RESISTANCE

Differences in proteins and enzymes would be expected between rust-susceptible and rust-resistant tissues. First, heritable resistance factors depend on genes which code for specific enzymes that ultimately prevent establishment of infection (Shaw, 1963). Second, various enzymes, particularly oxidases, have been associated with resistance mechanisms against many fungal diseases. Many workers have shown that the activity of certain enzymes rises in response to infection, especially in resistant plants (Metlitskii and Ozeretskovskaya, 1968). Many of the newly formed proteins are new isozymes of enzymes already present, particularly PPO, peroxidase, malic and succinic dehydrogenases, and acid and alkaline phosphatases. These new isozymes may be more resistant to fungal breakdown than the original enzyme or they may increase the effectiveness of fungitoxic substances.

Differences in proteins and isozymes have been associated with resistance to a number of plant diseases (Kiraly and Farkas, 1957; Kedar, 1959; Heitefuss *et al.*, 1960; Rudolph and Stahmann, 1964; Rubin, Ivanova, and Davydova, 1964; Andreev and Shaw, 1965; Fehrmann and Dimond, 1967; Sokolova and Zvyagintseva, 1968; Macko, Woodbury, and Stahmann, 1968). Other workers have not reported electrophoresis-pattern differences associated with resistance to tree rusts, but Koenigs (1966) reported cytochemical analyses for dehydrogenases in blister-rust infected *P. monticola* and *Ribes*.

Hare (1970) compared extracts from fusiform rust-resistant and -susceptible tissues for protein and isozyme patterns (zymograms) of 14 enzymes, by polyacrylamide-gel-disc electrophoresis. The purpose was to find a protein or isozyme that is always associated with resistance or susceptibility. Such a substance might be used as a genetic marker and, if identified as a specific enzyme, might provide a clue to a resistance mechanism.

Similar organs of all southern pines yield remarkably similar protein patterns, but several bands differ between similar susceptible and resistant tissues, e.g., the eastern and western loblolly seed source differences already described. Protein patterns from older resistant slash seedlings more closely resemble patterns from young resistant shortleaf than those from young susceptible slash.

Zymograms tend to vary more than protein patterns, perhaps because enzyme stains are frequently more sensitive than protein stains. Oxidases that may be important in disease-resistance mechanisms include IAAO, PPO, ascorbic acid oxidase, and peroxidase (Hare, 1966). Zymogram differences in all of these except IAAO have been shown between fusiform-rust resistant and susceptible southern pines (Hare, 1970). We have not succeeded in detecting the products of IAA oxidation on acrylamide gels, but this enzyme is apparently a form of peroxidase (Hare, 1964).

The role of PPO and IAAO in resistance and gall formation has already been discussed. Peroxidase may also oxidize phenols to more fungitoxic quinones in the presence of organic peroxides (Fehrmann and Dimond, 1967). Ascorbic acid is a strong reducing agent frequently found in the cell wall (Newcomb, 1963). It prevents the browning reaction following wounding by keeping the phenols reduced; thus it may decrease resistance by inhibiting PPO activity. Ascorbic acid oxidase, therefore, may promote resistance by its sparing action on the toxic quinones (Hare, 1970).

Several dehydrogenases have zymogram differences associated with fusiform rust resistance (Hare, 1970). Glucose-6-phosphate dehydrogenase participates in the pentose phosphate shunt, which is important in disease resistance (Farkas and Kiraly, 1962). Zymograms of this enzyme consistently differ depending on whether extract are from fusiform rust-resistant or -susceptible southern pines. Malic and alcohol dehydrogenases are also very active and have zymogram differences related to rust resistance.

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FLOOR DISCUSSION

The author could not be present to present this paper; it was offered only in abstract form by the moderator of the panel and there was no discussion.

ENVIRONMENT IN RELATION TO WHITE PINE BLISTER RUST INFECTION

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ABSTRACT

Pine trees can be free of blister rust infection either because they are growing in a climate unfavorable to rust or because they are genetically resistant to the rust. The climatic escape is hundreds of times more common than genetic resistance in the American white pines. The minimum time and temperature required for penetration by an isolate of the rice blast fungus (*Piricularia orizae*) differed significantly from one rice variety to another. This illustrates an interrelationship between environmental influences and genetic susceptibility. In the pine rusts, the minimum conditions for infection might, for example, be less limiting in sugar pine (*Pinus lambertiana*) than eastern white pine (*Pinus strobus*). As an example of local variation in blister rust incidence due to environmental differences, 29 Lake States plots with a median of 250 trees each were used. These were regularly examined for rust incidence for periods exceeding 10 years. In the 4 years prior to alternate host (*Ribes* spp.) eradication, the infection incidence on the 29 plots varied from 0 to 118 cankers/100 trees/yr. The mean was 67 cankers/100 trees. After eradication the variation was reduced and the infection incidence averaged 1.34 cankers/100 trees. In warmer zones, white pine blister rust is largely confined to locally cool, wet openings in the forest and at the bases of slopes. In cool zones the rust is more abundant when the pines are open to the sky in small openings. Trees escaping infection are usually under trees, in large openings, and where sea breezes carry the spores out over the water. Fusiform rust on slash pine was also favored in small openings and was rarer under overstories. It was rarest in large openings. Small openings are those that have diameters less than the height of the surrounding trees.

While I was at the University of Wisconsin in 1954, a reporter from the Milwaukee Journal called me and asked me about all those blister rust-resistant white pines I had found in southern Wisconsin. He thought it was wonderful that while Patton and Riker had found a few dozen resistant trees, I had found hundreds without rust. I tried to explain to him the difference between climatic escape and resistance. I was finding trees that had escaped from blister rust because the trees were growing in a climate unfavorable to blister rust, while Patton was finding trees that were genetically resistant to the rust.

I think I finally got the message across to this reporter. However, all of us working in the various phases of rust-spread research must keep the difference between genetic resistance and climatic escape firmly in mind. I, working in my environmental studies, must be aware of the variations in genetic susceptibility; you, in selecting trees resistant to the rust fungus, must be aware of the importance of microclimatic variations in small distances on the ability of the fungus to infect a particular host plant.

Considering genetics, most of the evidence seems to indicate less variation in pathogenicity in the fungus than there is variation in susceptibility and resistance in the host plants. However, this variation in host genetics affects the pathogenicity of the fungus. For an example from my own work, in an isolate of race 1 of the rice blast fungus (*Piricularia orizae* Cav.), infection occurred in 6 hours at 22°C on Zenith rice and in 6 hours at 20°C on C.I. 8970, an especially susceptible variety (Green, 1958; Green and Van Arsdel, 1956). This temperature difference was enough to affect epidemic development in a major way in Florida. Thus, the minimum environmental requirements for infection varied with the genetic susceptibility of the host.

While there are not similar data available on rust infection where one research worker has compared the same isolate on pines of different susceptibility, the published reports on white pine blister rust seem to indicate faster penetration and establishment on sugar pine (*Pinus lambertiana* Dougl.) than on eastern white pine (*P. strobus* L.). With these bits of evidence in mind, I think we have to assume that minimum environmental requirements for infection can vary from host to host with their genetic susceptibility, and that environmental and genetic effects are always closely linked.

However, Patton's work on selecting resistant trees and mine on microclimate, in the same region on the same rust on the same host species (*P. strobus*), indicate that genetic and microclimatically controlled factors of susceptiblity and pathogenicity can be effectively and profitably separated. Microclimates do affect the amount of host infection, regardless of the overall susceptibility of a species to a rust: a tree in a moist site should always become infected more readily than its adjacent neighbors in drier sites. When selecting resistant candi dates you should be sure you have not selected an equally susceptible host located in a microclimate unfavorable to infection.

While most of my examples will come from work on white pine blister rust, I shall give sufficient examples to show that fusiform rust infection is much more prevalent on slash pines in moist sites than on drier sites in the same pine stand.

LOCAL VARIATION IN BLISTER RUST INCIDENCE

We can look at any mass of infection incidence data and make a pretty good estimate of how much climatic variation is occurring in the infection process. As an example we can take the masses of infection data collected in the Lake States by E. E. Honey, H. N. Putnam, Ray Weber and others that I presented at the First International Phytopathology Congress in London last year.

The variation is tremendous between the 29 stands prior to eradication (18 of these stands are shown in Fig. 1). The pre-eradication incidence of rust ranged from no cankers per 100 trees to the greatest infection in a given year of 118 cankers per 100 trees. This variation can be ascribed to environmental differences since all stands had abundant ribes present. The number of repeatedly observed sample trees was adequate. The median number was about 250 trees per stand, with the range in individual stands from 75 to 1,500 trees. After eradication, nearly all of the variation was removed since all plots had less than 20 cankers per 100 trees and all but two had less than 5 cankers per 100 trees.

Incidentally, the total results of 5,174 cankers in the four years prior to eradication (67 per 100 trees) compared to 103 cankers in the four years after eradication (1.34 per 100 trees) was significant at the 1 in 1000 level (Van Arsdel, 1968).

Almost any series of infection plots will show variation in the infection level. The question is, can we systematize this variation so we can predict where the heavy, light, and lack of infection will occur? The answer is: we can.

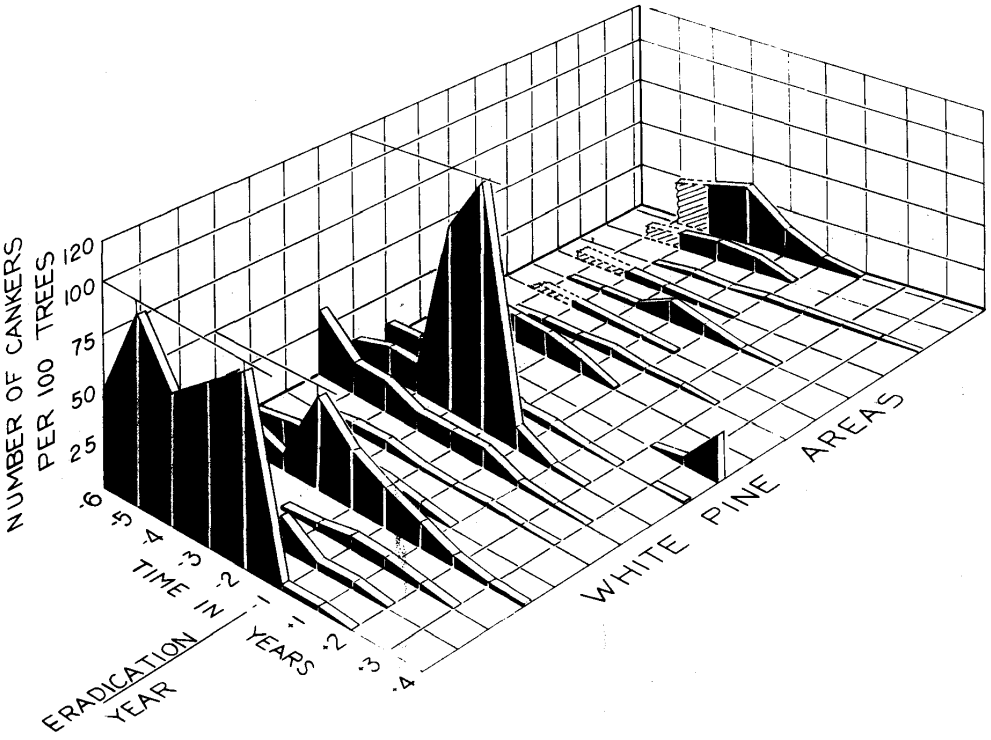


Figure 1. Differences in the amount of blister rust infection occurring on 18 of 29 study areas.

PREDICTION OF MICROCLIMATES FAVORABLE AND UNFAVORABLE TO RUST

The white pine blister rust fungus (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) is sharply limited by meteorological factors in the eastern United States (Charlton, 1963; Van Arsdel, Riker, and Patton, 1956).

In the Lake States, climate largely determines the distribution of rust. For convenience the disease distributions can be divided into three scales according to meteorological conditions: (1) a macro scale that is determined mainly by latitude and mass area elevation, (2) a meso scale that is determined by elevation range of hills and river valleys, and (3) a micro scale that is determined by the structure of forest stands and the influence of small hills and slopes within the stand (Van Arsdel, 1965a).

In the large-scale climatic gradation, rust is more general and found on white pines (*P. strobus*) on all sites in the more northern regions, at higher elevations, and near cold bodies of water such as Lake Superior (Van Arsdel, 1961, 1964). This is shown as zone 4 in Fig. 2.

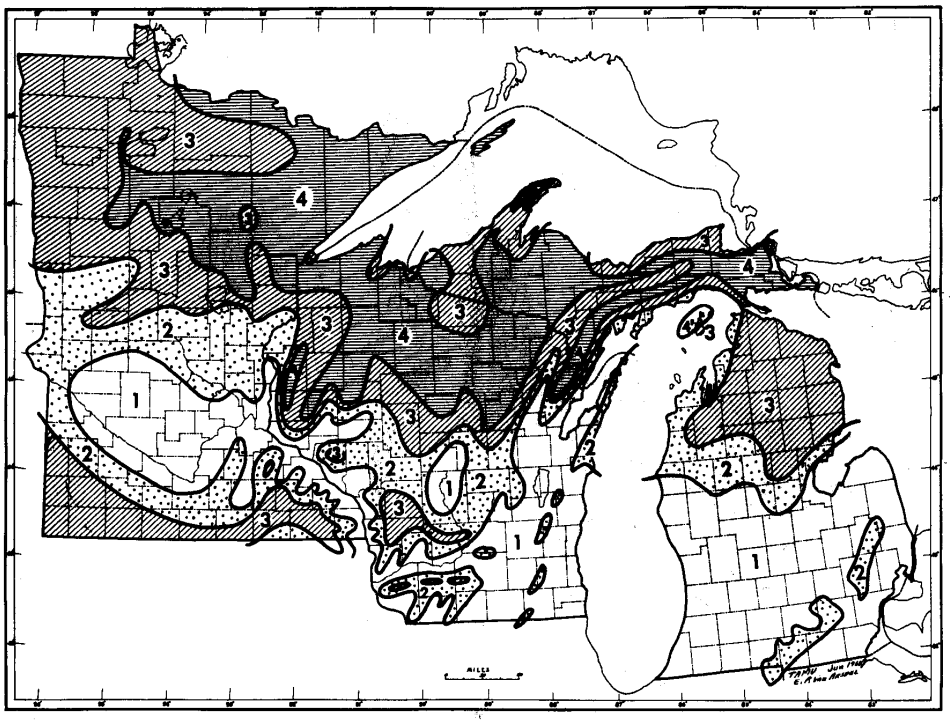


Figure 2. Map showing differences in quantity of blister rust spread to white pines in the Lake States. Rust in tops of emergent pines carried from distant ribes are characteristic of Zone 4. The cooler the summer weather, the more favorable for disease spread.

In the mesoclimatic scale, the hill-valley structures are superimposed on the macroclimatic scale and modify the large-scale distribution. Rust is more prevalent at high elevations and scarce in broad river valleys (Van Arsdel, Parmeter, and Riker, 1957).

In the microclimatic scale, the stand structure and small topographic features are superimposed on the mesoclimatic scale and further modify the climatic distribution. The bases of slopes, small narrow valleys, and small openings in the crown cover of the forest have abundant rust. Zone 1 in the map in Fig. 2 shows where rust is found only in these cool wet sites. Shoulders of hills and large openings in the forest have less rust on the pines (Van Arsdel *et al.*, 1961). The meteorological forces that cause locally cool wet places are illustrated in Fig. 3.

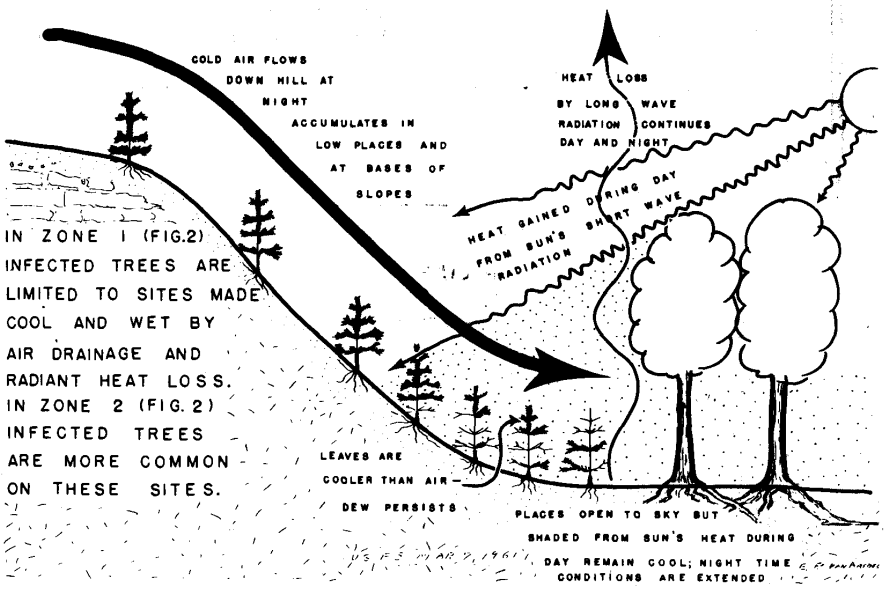


Figure 3. Drainage of cold air at night and radiant heat loss make locally cool wet spots.

The patterns of climate-controlled rust distribution are determined by temperature and moisture effects on the production of spores, the duration of spore viability, the germination of spores, the penetration into the host, and the establishment in the host. The patterns of spore dispersal are controlled by night air circulation.

RADIATION EFFECTS--FOREST OPENINGS

The opening in the crown cover of the forest serves as a good example of the influence of radiation patterns modified by vegetation on the epidemiology of the disease. An opening in the forest is subject to strong radiational influence because the surrounding forest breaks the wind and minimizes its effect (Geiger, 1950).

A forest opening with a diameter greater than the height of the surrounding trees is hotter by day and cooler by night than either open fields or the surrounding forest. The extent of this diurnal temperature variation depends on the ratio of the diameter of the opening to the height of the surrounding trees (Fig. 4) (Van Arsdel, Stearns, and Main, 1968; Geiger, 1950). Frequently, the daily temperature range is increased by 8°C. *Ribes* spp. (gooseberries and currants) growing in these larger-sized openings do not have blister rust present on their leaves. In the northern Lake States, minimum summer night temperatures in such openings are usually below 5°C and often below freezing. This temperature is too low for either aeciospores or urediospore infection of the ribes. Daytime temperatures are often greater than 35°C (see Fig. 5)(Van Arsdel *et al.*, 1968). The blister rust mycelium in the leaf generally does not survive under such high temperature regimes. These larger openings are both too hot and too cold for rust infection on ribes. They are also too hot for sporidial germination and infection on white pines.

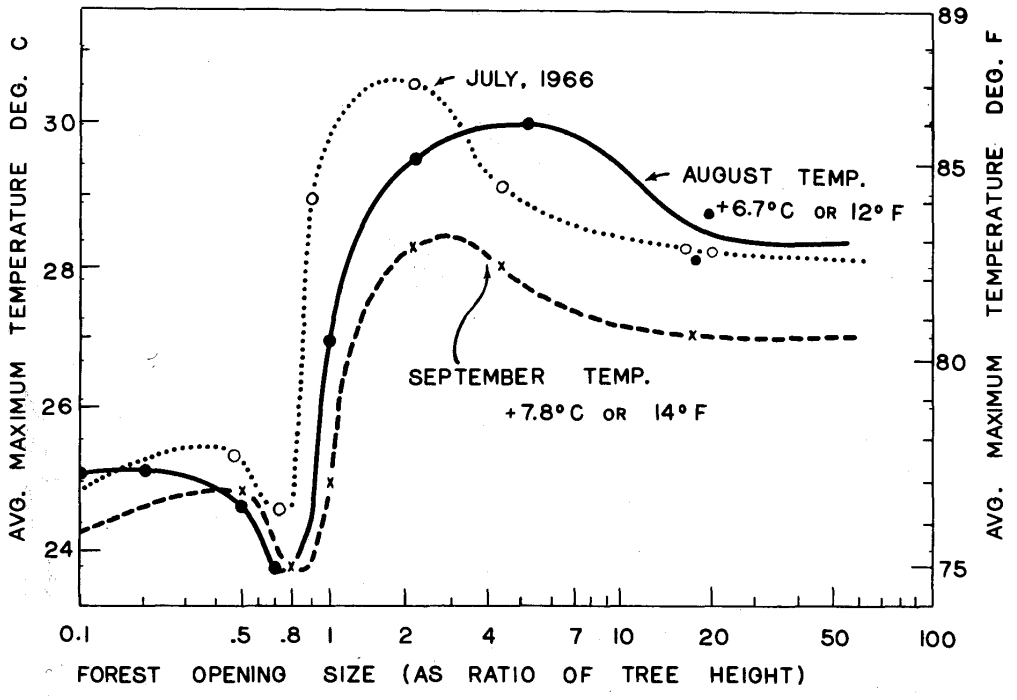


Figure 4. The relative effects of circular forest opening diameter and air temperature in the center of the opening (18" above the ground).

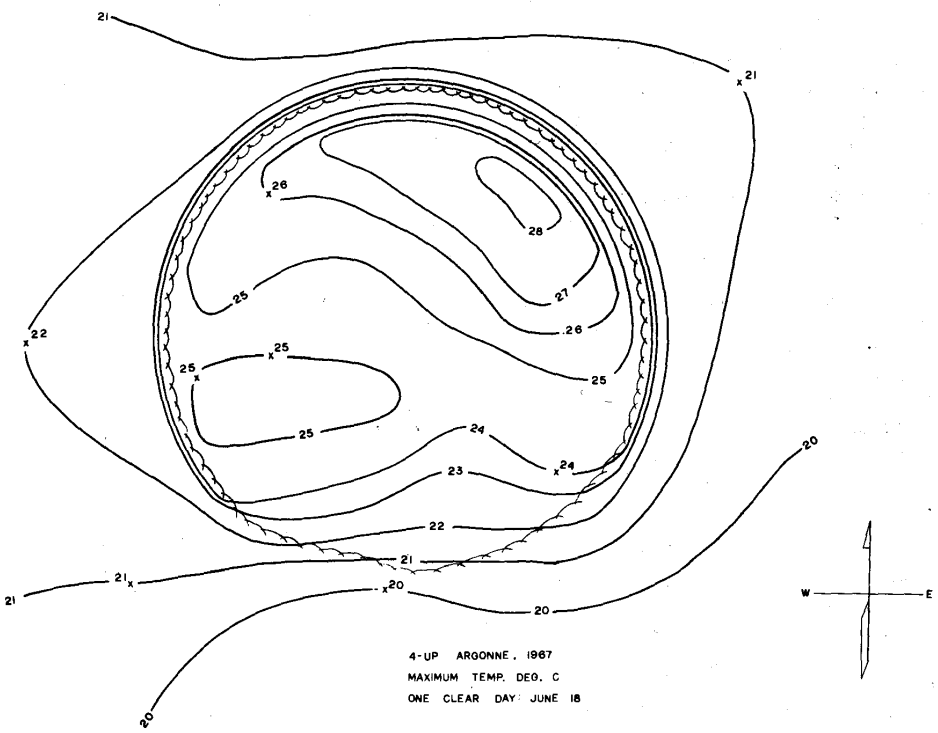


Figure 5. Temperature variations in a forest opening 280 ft. in diameter in 70 ft. tall trees (4:1::D:H ratio). The 8°C warming above the shade temperature would raise a July or August day temperature of 27°C to 35°C--a temperature fatal to blister rust.

In smaller openings with a diameter half the height of the surrounding trees, the opposite is true. In the Lake States the sun never shines onto the ground in such an opening after August 10. Consequently, the ground is always cooler during the day than on nearby open-field or tree-covered sites. It is warmer at night because the closely surrounding trees hold in the heat and impair outward radiation. The plants growing in the opening are side-shaded from insolation and are generally cooler than the surrounding air because of their radiant heat loss to the open sky. This means that the cooled plants are often cooler than the dew point, and dew periods are greatly extended. The locally supercooled air also increases available moisture. Thus, the small opening has a cool, very wet, local climate with a reduced temperature range that is extremely favorable to rust infections on ribes, teliospore and sporidial production on ribes, and sporidial infection on white pine.

Except for small openings and a few other especially favorable sites described later, rust is rarely present in Zone 1, Fig. 2. On pines in small openings in the southern Lake States, rust is almost invariably present. In the northern Lake States where the macroclimate is more

favorable for rust, such small openings frequently contain only the carcasses of dead trees. Other rusts, such as *Coleosporium* needle rust on red pine, are concentrated in small openings. Similarly, in an East Texas area on 35, 1/100th-acre plots, the 14 in small openings averaged 77 fusiform rust cankers per 100 slash pine trees, the 2 in large openings averaged 7 cankers per 100 trees, and the 12 under a pine overstory averaged 12 cankers per 100 trees. All 1/100th-acre plots had oak present. This high incidence of rust on pines in small openings depends to a greater extent on the high moisture than on the favorable temperature. On the other hand, white pines under thin canopies such as aspen have very little rust throughout the Lake States.

These observations, coupled with tests where additional moisture was added, indicate that condensed water on super-cooled leaves is most favorable to rust infection. Whereas much has been written about the relation of spore germination to relative humidity, few workers have considered what relative humidity might mean under a given set of field conditions. Rogers (1957), in his work on snapdragon rust, did consider moisture conditions other than humidity. He showed that under dew-forming conditions when the leaf is colder than the air, the water formed on leaves at 85% relative humidity. Wellington (1950), in his studies of the effects of radiation on the temperatures of insectan habitats showed that leaves can be 10°C warmer or 2°C cooler than the surrounding air. These observations show that the ability of the spores to infect the plant depends not so much on the relative humidity of the air as on whether the temperature of the leaf is below the dew point. Regardless of relative humidity, when the temperature of the leaf is below the dew point of the ambient air, there will be dew on the surfaces of the leaf and the adhering spores. Except for short periods before the dew dries off in the morning, when leaf temperature is above the dew point there will be no free water on leaf undersurfaces, even in rain. In the general forest, pines out from under the overstory crowns in the small openings will have many times more rust than their tree-covered neighbors.

Some interesting information that emphaszes these radiation-temperature-moisture relationships was collected as a part of systemic fungicide study. Data on the compass direction of the canker from the center of the tree, collected for several thousand cankers, showed that cankers were not distributed randomly. Most of them were on the west side of the tree opposite the rising sun where dew could persist a little longer. Cankers are also slightly more abundant on west slopes and to the west of a radiation obstacle like a forest edge.

AIR DRAINAGE--SLOPE EFFECTS

Local topographic variation influences microclimate to favor or hinder rust infection. Cliffs and steeper hills interrupt incoming radiation in the manner previously described for trees. However, this local radiation effect by hills is mostly a daytime phenomenon. More important to the night-spreading blister rust fungus are the air-drainage influences of these slopes. Cold air accumulates at the bases of hills and flows away from the shoulders, making a warm slope at the top of the hill and a cold pool at the base. Where the bases of two hills come together in a narrow valley, a very cold pool accumulates (and often starts a down-valley wind). In southwestern Wisconsin where the general climate is too warm for blister rust spread, rust infection is usually present in these cold pools (Van Arsdel *et al.*, 1961).

COMBINED EFFECTS

In the southern part of the Lake States, these vegetative radiation and topographic air-drainage influences reinforce each other and add to the incidence of rust where small openings are in valleys. A formula constructed by adding together these features for a site gave a guide that permitted prediction of rust presence or absence with an 89% accuracy in southwestern Wisconsin. Absence of rust where it was predicted occurred 10% of the time. Infections occurred where not predicted only 1% of the time (Van Arsdel, *et al.*, 1961).

NIGHT BREEZES--LAKE DRAINAGE WINDS

A more difficult concept to understand is the distribution of rust in specific patterns because of the paths taken by certain nocturnal breezes. The night breeze distribution control is noted only in the coolest and wettest areas of the Lake States where the climate is most favorable to the rust fungus. Near the Great Lakes, night breezes have been implicated as carriers of the pine-infecting spores. These 2-mph breezes develop as a result of the differences between the water temperatures of Lakes Michigan and Superior and the land temperature on the 40-mile-wide strip of land between them. The study area was a part of Michigan's Upper Peninsula.

As the land gets cold at night, adjacent cooled air moves in a low, cold flow out over the warmer lake. Spores released from currant bushes less than 5 miles from the lake are usually carried out over the water by this breeze. Thus, pines near the lakes are seldom infected. Above this cold flow a reverse flow carries the warmer lake air over the land. Updrafts over smaller local spots of warm air, such as occur over swamps, forests, and small lakes, loft some spores to this backflow level. The backflow carries these spores to a strip approximately 7 miles wide and 10 to 17 miles from the lake, where they are carried down by a downdraft. These spores infect pines as much as 5 miles from the nearest currant bushes and even infect them high in the crowns. The map in Fig. 6 shows the rust distribution on pines; the chart shows a diagram of the flow.

Although we have not traced the spores all the way along this path, we have watched the lake breeze carry smoke and balloons along the way. We know the spores have 5 hours to move (before light kills them) in a breeze of 2 mph, so they can go 10 miles. This movement just fits the pattern of rust infections in the past 20 years (Van Arsdel, 1963). Breezes around smaller lakes carry spores in similar patterns.

Other night winds that affect local rust distributions are down-valley winds and reverse flows from down-slope winds on valley slopes. The larger scale backflow spore impact areas can be seen in the map in Fig. 2. Slope winds into swamps and their reverse flows located 15 to 25 ft above the ground are also important in placing rust infections (Van Arsdel, 1958). Fig. 7 shows a typical swamp-slope air movement.

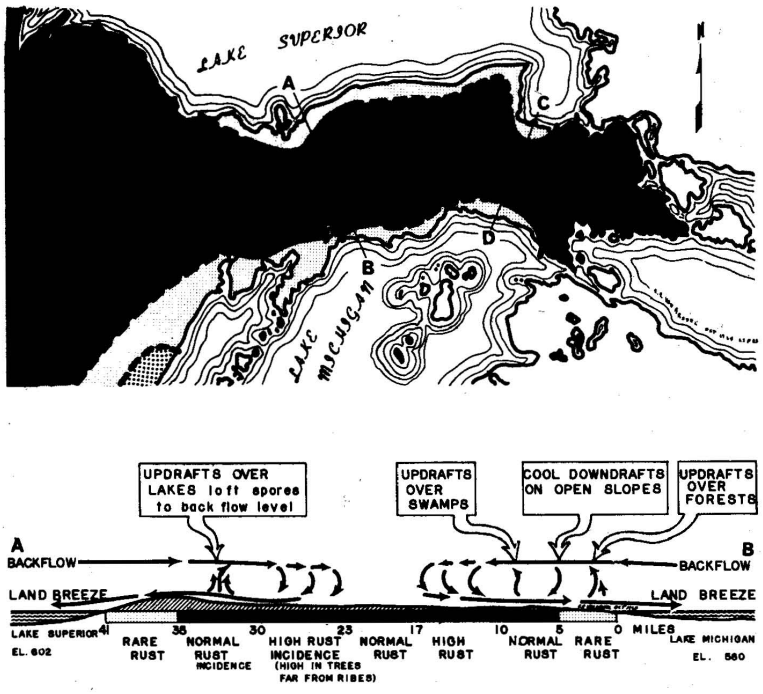


Figure 6. Map of eastern Upper Michigan showing areas of high blister rust (high in trees, far from ribes). Darkest area has high rust. Lower diagram shows cross section of airflows controlling rust spread in this area.

FOREST EDGES

A number of tests have shown that a specific air-current relation exists at the edge of a woods. Air flows near the ground from the open area into the woods, up under the crowns in an updraft, and then back out into the open area. Rust spores travel in a warm backflow layer that extends from under the tops of the crowns out into the open, where a down-draft may eventually bring them down (Van Arsdel, 1958).

For example, in northeastern Minnesota (Fig. 8), at the top of a divide that slopes down to Lake Superior, we planted white pine trees in an open field surrounded by 35- to 45-ft aspens (*Populus tremuloides* Michx.). The pines in the center of the field developed 50 times as much rust as those near the edges (Van Arsdel, 1965b).

A long area of heavy rust concentration in the center of the field paralleled the edges of the taller forests on two sides of the plot. Yet, alternate hosts were distributed throughout the field and in the surrounding woods. The rust distribution in this field was exactly what would be expected if the spores were all carried by air currents in two opposing cells going into the surrounding hardwoods (away from the center

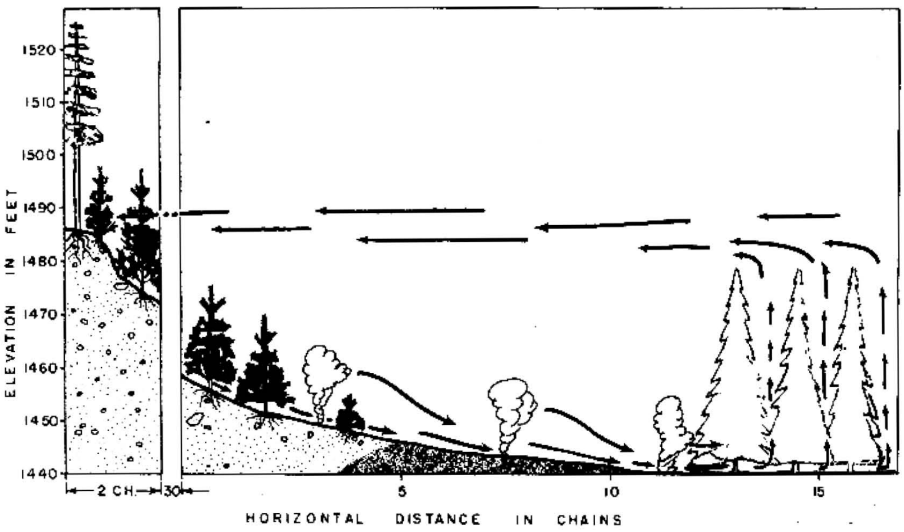


Figure 7. Pattern of airflow that controls rust spread around a swamp edge.

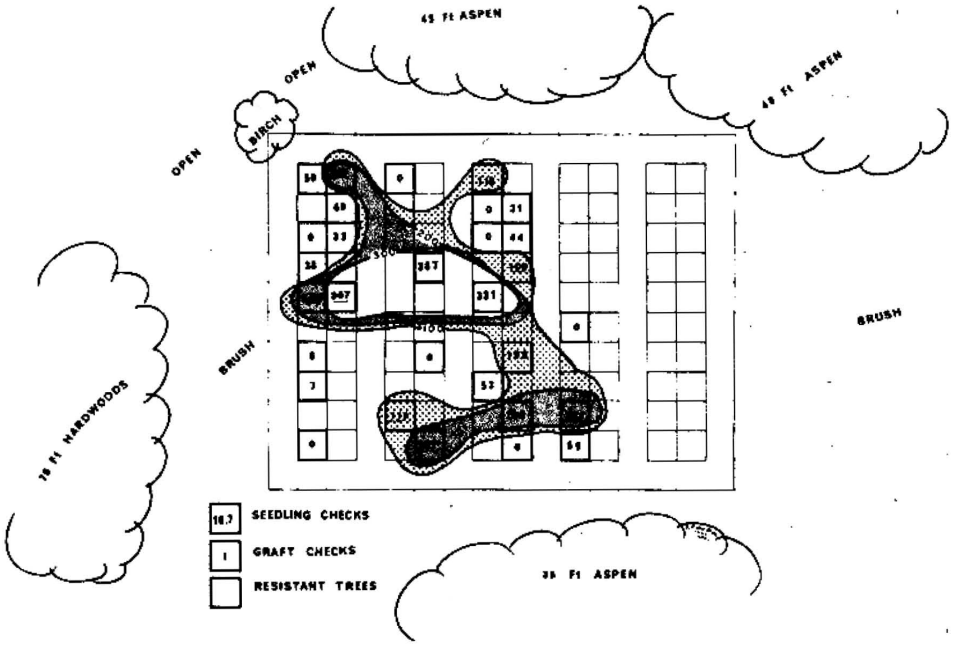


Figure 8. Numbers of blister rust cankers per 100 white pine seedlings (2-3 ft tall) in a forest opening at Whyte, Minn. Legend boxes show average infection rates. Graft check plot values have been multiplied by 16.7 to arrive at a corrected infection index for the graft canker plots.

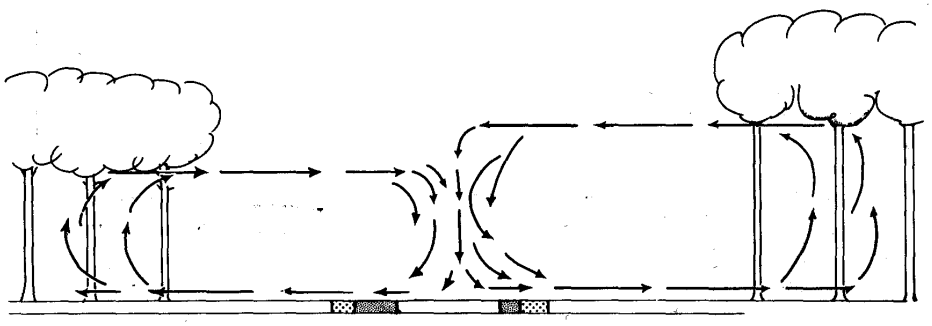


Figure 9. Diagram of an air circulation explaining the rust distribution in Fig. 8.

of the field), then up through the hardwoods and back to the center of the field where a downdraft occurred (Fig. 9). In two similar openings in northeastern Wisconsin, I have observed smoke flows in this pattern on four occasions at dawn (Van Arsdel, 1967).

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FLOOR DISCUSSION

KREBILL: The one thing that does concern me about your work is that it seems to relate mostly to the clear weather situation while earlier workers put more emphasis on the importance of precipitation. Would you care to comment further about the importance of precipitation in dissemination of basidiospores of *C. ribicola*?

VAN ARSDEL: In the Lake States, you have to have precipitation involved. You have to have a couple of wet days to get enough moisture, but in a rainy, cloudy situation, you do not get condensation on the telia on the bottom of the ribes leaf, therefore, it's not wet enough for release of sporidia. For the release of sporidia, you have to put an agar plate near the leaf and supply extra water or provide another source of moisture in rainy weather. So the release actually occurs when it clears off; when the leaves become cooler than the air and the water condenses on the under side of the leaf. So it does occur in clear weather between rainy spells at night rather than when it's actually raining. I put an awful lot of observations into that, and this is my understanding of how it works now.

ZUFA: You mentioned in conversation that nitrogen affected the susceptibility to the rust. We have made a similar observation. Could you add anything to these observations?

VAN ARSDEL: Well, there is a lot of work on *Piricularia* and various rusts. I didn't want to get into it too much. I haven't made a specific review, but there is quite a bit of information available. Richard F. Watt of the Forest Service North Central Forest Experiment Station found this on his fertilizer plots with *Chrysomyxa* in black spruce in the Lake States. Pure nitrogen does increase susceptibility, and this is something I have just accepted from my years of work with the rust. It's sort of like putting corn on a fertile field. It grows better than corn on a poor field. The rust is an obligate parasite, and if you make the host a little healthier, it grows better.

ZUFA: I wonder if this really increases the susceptibility or if the rust was already in the tree living with it in a kind of symbiosis, and the nitrogen affected only the appearance of the blisters. We had trees on which blister rust did not show up even after repeated inoculations, but 5 to 6 years later when a nitrogen fertilizer was applied on such trees the blisters suddenly appeared.

VAN ARSDEL: I think that probably you are right; the fungus needs nitrogen, and is higher in protein than the host material. At least, those rodents that chew on cankers all the time are after something. I think they are after protein nutrition (or nitrogen). It shouldn't be too difficult to analyze but I haven't done it.

WEISSENBERG: In discussing the question of potential hazard areas for blister rust, the Mediterranean countries have been mentioned. Miss Emma Vecchi de Pellati mentioned at the FAO 2nd World Consultation on Forest Genetics that the white pine blister rust has not occurred in Italy although they have both the alternate host and *P. griffithii* (syn. *P. wallichiana*) and *P. strobus*. And Prof. Vidacovic mentioned that the rust does not occur in Yugoslavia. I would like to know whether these areas can at all be considered potential hazard areas. They might have both hosts occurring sympatrically but the climate might not be suitable for the total life cycle of the rust.

VAN ARSDEL: Spaulding showed quite a gradation across Europe in his paper of 1929 on conditions of rust in Europe. Harm has been done, I think, to research work in the U.S. Forest Service, because people that went to Switzerland were told by a Swiss forester that the rust wasn't very serious. "We grow *P. strobus* and we get rust but it never hurts anything." Yugoslavia is in a warm climatic zone and I don't think you could grow the rust in it if you wanted to, anymore than you could in southwest Texas, Ohio, or Indiana. I haven't explained the mechanism of what happens after a little rust gets into an area. Warmer weather is required for urediospores to make a secondary spread after the initial ribes infections from a few cankers on pines. They spread rapidly from ribes leaf to ribes leaf, defoliating them in warm weather. When the cooler weather that permits telial formation and germination comes in the fall, there are no ribes leaves with rust on them to infect more pines. Thus the rust is controlling itself. Farther north most infections on ribes come from aeciospores on pines, without much uredial infection occurring. The aeciospore to teliospore cycle occurs in the cooler climates. The warm weather, heavy urediospore spread that occurs in the warmer Lake States seems to occur in the western U.S. The same type of infection gradient probably occurs in Europe--high rust incidence in the cool north, low rust incidence in the cooler part of the south.

SCHÜTT: Dr. Van Arsdel, you stated that we know that basidiospores have only about 4 hours to germinate and penetrate before light kills them. This is a very important factor since it could be useful in understanding an early resistance mechanism.

VAN ARSDEL: I think I'd better correct this. Many times the sporidia have only 4-5 hours to reach the pine. Now let's get a point first. I'm talking about epidemics. I'm not talking about the one or two in a hundred ifnections, or the case when Ray Hirt says the spores would live through a single hot day, he pointed out that 3 out of 10,000 lived through the day. I'm not talking about this kind of situation. I'm talking about epidemic situations. You may release a lot of rust spores, and some will live through the next day. Most of them in most climates, cannot live through the next day. There have been a lot of tests, some very bad, in which they put a few dry spores on a glass slide, and let the sun shine on it, and they died. You might die, too, but there is a difference. When I worked out the gradients from zones of ribes out into the pine area I found two gradients of spores. They are related to how long it takes for the number of infections to take the square root of itself at a given

distance. With increasing distance the rust infection follows an exponential curve. In British Columbia, according to the published papers by Kimmey and Buchanan, and some in Kittery Point, Maine, this distance is about 25 feet. In northern Minnesota, in upper Michigan, and in northern Wisconsin, this distance is 300 feet. Now, according to prior work, this has to say that something in the environment is allowing these spores to go much, much farther, or a much greater proportion of them are living to cause infections. I wonder if maybe this isn't the case in areas where it's so cold and so wet and so cloudy so much of the time that a spore can live more than a single night in these areas and maybe this is why the hazard is so much higher. I said in one of my papers that maybe it's a jump to this zone instead of a climatic gradient. I think this might be where the sporidia might live one day, or more than one day.

HOST RESPONSE OF PINES TO VARIOUS ISOLATES OF *CRONARTIUM QUERCUUM* AND *CRONARTIUM FUSIFORME*

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ABSTRACT

When pines of five species were uniformly inoculated with isolates of *Cronartium quercuum* and *C. fusiforme*, differences in susceptibility of the trees to three geographic sources of *C. quercuum* were observed during the first year. *Pinus elliottii* and *P. banksiana* were susceptible to Wisconsin isolates; *P. taeda* and *P. clausa* to North Carolina isolates; and *P. elliottii*, *P. taeda*, *P. echinata*, and *P. banksiana* to Mississippi isolates. In the *C. fusiforme* inoculations, the hosts responded similarly to four isolates from various Mississippi sources. Gall shape and recovery from symptoms also varied among geographic sources of *C. quercuum*. *C. quercuum* could be distinguished from *C. fusiforme* by gall shape and by host range. These results establish that races of *C. quercuum* exist. They also confirm previous research indicating that response of the pine host can be used to distinguish the two species of *Cronartium*.

The geographic range of *Cronartium fusiforme* Hedgc. & Hunt ex Cumm. is overlapped almost completely by the range of *Cronartium quercuum* (Berk.) Miyabe ex Shirai. The former of these two pine-oak rust fungi is the most serious pest of southern pines, while the latter is relatively minor in the South. Morphologically the two species are considered to be identical. Although both serological (Gooding and Power, 1965) and histological (Jewell and Walker, 1965) differences have been observed, the best distinction is still considered to be gall shape (Peterson, 1967). Following Hedgcock and Siggers (1949), galls of *C. quercuum* are regarded as primarily spheroid, while *C. fusiforme* galls are always elongated and usually fusiform. The only other distinguishing feature is the species of pine attacked. Some southern pines are susceptible to both fungi, some to only one, and some to neither (Arthur, 1962).

In the research reported here, the validity of these methods of differentiation was reassessed on the hypothesis that geographic variation exists within the species of *Cronartium*.

MATERIALS AND METHODS

Six isolates of *C. quercuum* and four isolates of *C. fusiforme* were collected in the spring of 1967. Two isolates of *C. quercuum* were from each of three sources: Jack pine, *Pinus banksiana* Lamb., in Wisconsin; Virginia pine, *P. virginiana* Mill., in North Carolina; and shortleaf pine, *P. echinata* Mill., in Mississippi. The four isolates of *C. fusiforme* were obtained from slash pine (*P. elliottii* var.*elliottii* Engelm.) and loblolly pine (*P. taeda* L.) in Mississippi The spore collections were sifted over a 74μ screen, dried over calcium chloride, and stored in a refrigerator at 5°C until used. Telia were obtained by inoculating water oak (*Quercus nigra* L.) seedlings with aeciospores approximately 2 weeks before the telia were to be used.

Pines of five species were grown from seed and inoculated with each of the 10 isolates. The pine species were: slash and loblolly pine (both from Mississippi seed sources), shortleaf pine (Tennessee seed source), jack pine (Wisconsin seed source), and sand pine (*P. clausa* (Chapm.) Vasey, Florida seed source). The seedlings were started in 2-inch peat pots in a greenhouse, and after 8 to 12 weeks were inoculated and transferred to 4-inch pots. They were kept in the greenhouse for 6 months after inoculation and then in a lathhouse for another 6 months.

The apparatus for inoculating the pines has been described previously (Snow, 1968; Snow and Kais[1]). The telia from one isolate of *Cronartium* were introduced into the apparatus on a given day and 16 seedlings of each species of pine were then inoculated. Spore deposition on the plants was regulated by adjusting airflow and time of seedling exposure. The spore count, measured on glass cover slips, was adjusted to 30 to 60 spores/mm^2. It was maintained at this level by calibration and readjustment every 5 to 10 minutes. After the pine seedlings had been inoculated, they were incubated in moist chambers for 48 hours. The inoculations were begun on June 29, 1967, and were completed by August 29, 1967. Isolates were selected randomly for each inoculation date.

The criteria for comparing the isolates were the occurrence of galls and the size and shape of galls 12 months after inoculation. Galls were readily apparent at 6 months, but some hosts recovered after that.

RESULTS

There were significant differences (0.05 level) in percentage of the pine hosts developing galls after inoculation with the isolates of *C. quercuum* from the three geographic sources. Slash pine was moderately susceptible to the Wisconsin and Mississippi isolates but moderately resistant to the isolates from North Carolina (Fig. 1). Loblolly pine was moderately susceptible to the isolates from Mississippi and North Carolina, but was extremely resistant to the isolates from Wisconsin. Shortleaf pine was susceptible only to the *C. quercuum* isolates from Mississippi. Jack pine was extremely susceptible to the one Wisconsin isolate (the jack pines assigned to the other Wisconsin isolate died prior to inoculation) but moderately resistant to the Mississippi isolates and extremely resistant to the North Carolina isolates. Sand pine was

[1] *Paper presented in these proceedings.*

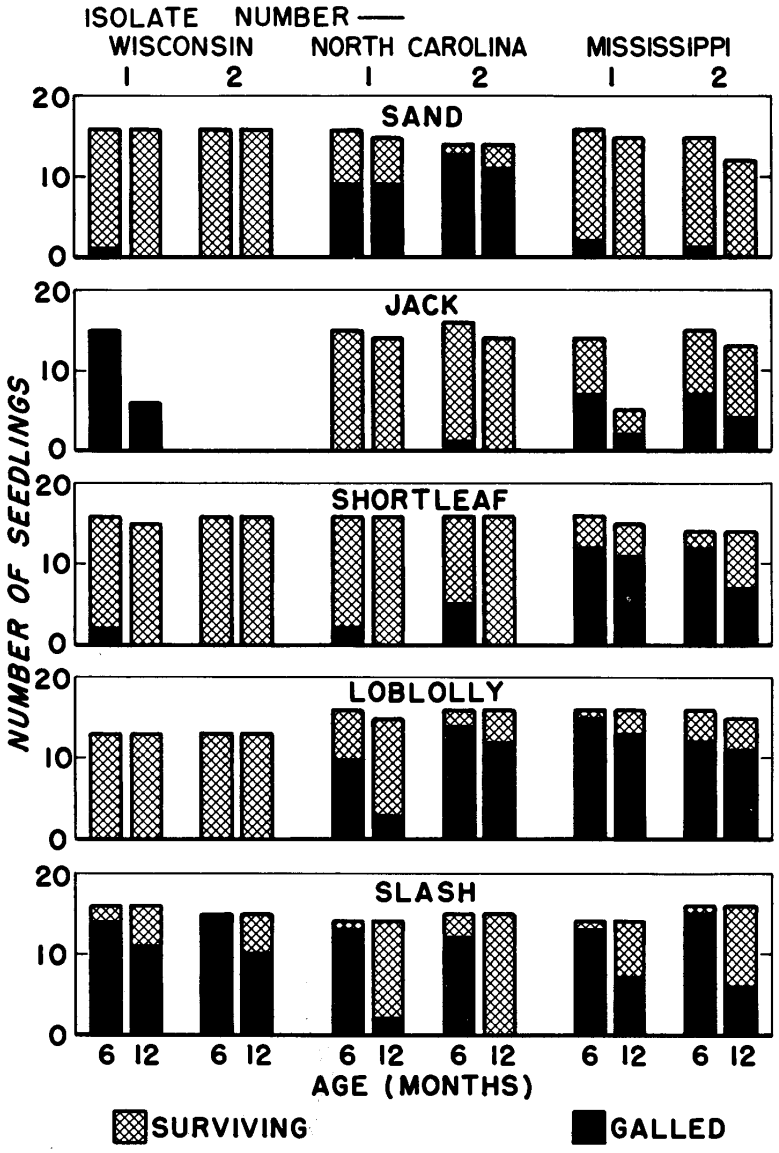


Figure 1. Gall development on pines inoculated with *Cronartium quercuum* from three geographic sources.

moderately susceptible to the North Carolina isolates but extremely resistant to the Mississippi and Wisconsin isolates.

An analysis of variance for proportion of plants with galls at 12 months showed a significant interaction between the five species of pine and the three geographic sources of *C. quercuum*.

The shape of galls on the pines inoculated with the *C. quercuum* isolates can be compared by examining the ratio of gall diameter to gall length (D/L ratio) in Table 1. The larger this ratio, the more globose the gall. Almost always, the ratio increased markedly between 6 months and 12 months.

Table 1. Mean ratio of gall diameter/gall length 6 and 12 months after inoculation with *C. quercuum* isolates.

Pine host and month	Geographic sources: Wisconsin 1	Wisconsin 2	North Carolina 1	North Carolina 2	Mississippi 1	Mississippi 2
Sand						
6	0.16 (1)[a]	---[b]	0.30 (9)	0.27 (13)	0.20 (2)	0.22 (1)
12	---	---	.86 (9)	.66 (11)	---	---
Jack						
6	.26 (15)	[c]	---	.75 (1)	.48 (7)	.41 (7)
12	.65 (6)	[c]	---	---	.91 (2)	.86 (4)
Shortleaf						
6	.22 (2)	---	.18 (2)	.20 (5)	.42 (12)	.40 (12)
12	---	---	---	---	.72 (11)	.95 (7)
Loblolly						
6	---	---	.12 (10)	.18 (14)	.51 (15)	.38 (12)
12	---	---	.33 (3)	.39 (12)	.88 (13)	.95 (11)
Slash						
6	.13 (14)	.15 (15)	.18 (13)	.12 (12)	.25 (13)	.20 (15)
12	.29 (11)	.40 (10)	.58 (2)	---	.51 (7)	.46 (6)

[a] Numbers of plants with galls shown in parentheses.
[b] Dashed lines indicate that no plants had galls.
[c] No test.

At 12 months there were no obvious differences in the reactions of the pines to the four isolates of *C. fusiforme* (Fig. 2). Slash and loblolly pine were extremely susceptible, while shortleaf, jack, and sand pine were resistant to all four isolates. The susceptible pines inoculated with the *C. fusiforme* isolates usually formed only fusiform galls (Table 2)

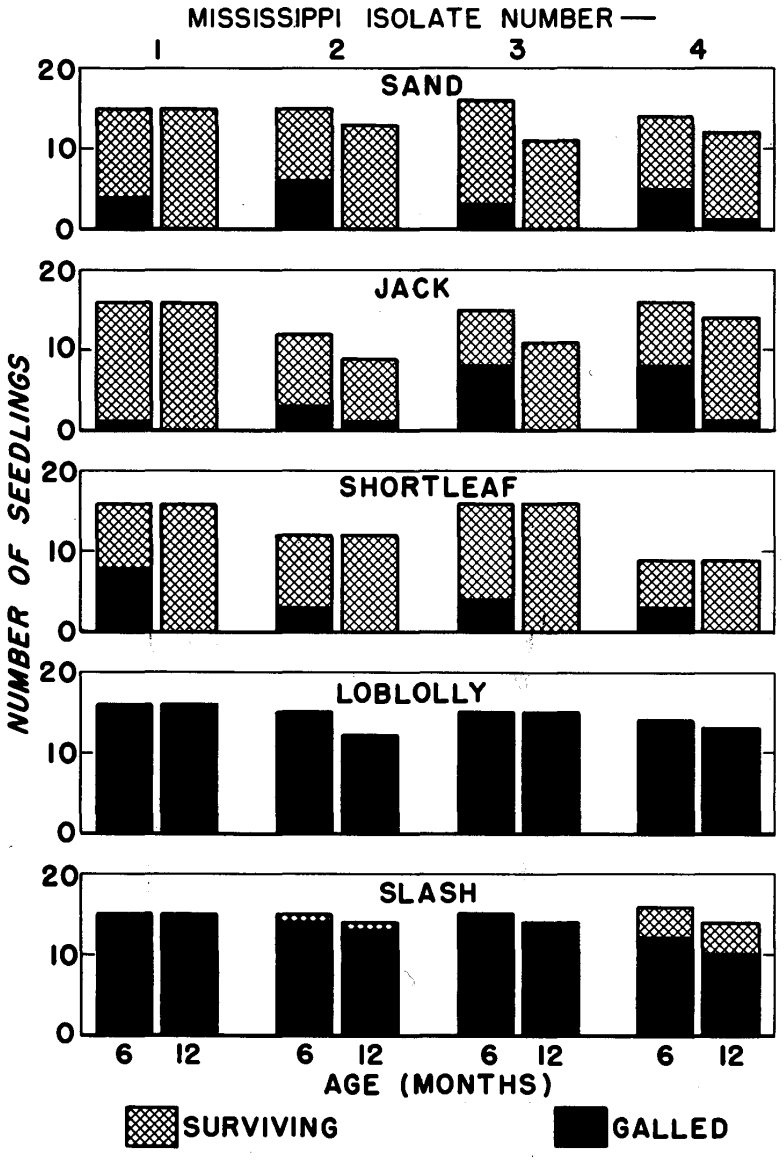


Figure 2. Gall development on pines inoculated with four Mississippi isolates of *Cronartium fusiforme*.

which were almost all very large and uniform in shape. The D/L ratios were consistently lower than for the *C. quercuum* galls and changed little between 6 and 12 months.

Table 2. Mean ratio of gall diameter/gall length 6 and 12 months after inoculation with *C. fusiforme* isolates

Pine host and month	Mississippi isolates 1	2	3	4
Sand				
6	0.17 (4)[a]	0.17 (6)	0.15 (3)	0.21 (5)
12	---[b]	---	---	.29 (1)
Jack				
6	.19 (1)	.24 (3)	.19 (8)	.30 (8)
12	---	.69 (1)	---	.39 (1)
Shortleaf				
6	.18 (8)	.19 (3)	.17 (4)	.20 (3)
12	---	---	---	---
Loblolly				
6	.12 (16)	.13 (15)	.11 (15)	.13 (14)
12	.12 (16)	.17 (12)	.13 (15)	.12 (13)
Slash				
6	.12 (15)	.15 (14)	.11 (15)	.12 (12)
12	.15 (15)	.14 (13)	.13 (14)	.13 (10)

[a] Numbers of plants with galls shown in parentheses.
[b] Dashed lines indicate that no plants had galls.

Figure 3 illustrates reactions of various pine species to the different isolates of *Cronartium*. Most responded in a uniform manner to inoculation with individual isolates of either fungus species. Exceptions to this were loblolly and sand pine, which, when inoculated with North Carolina No. 2 isolate of *C. quercuum*, formed galls of both types (Fig. 3G,H).

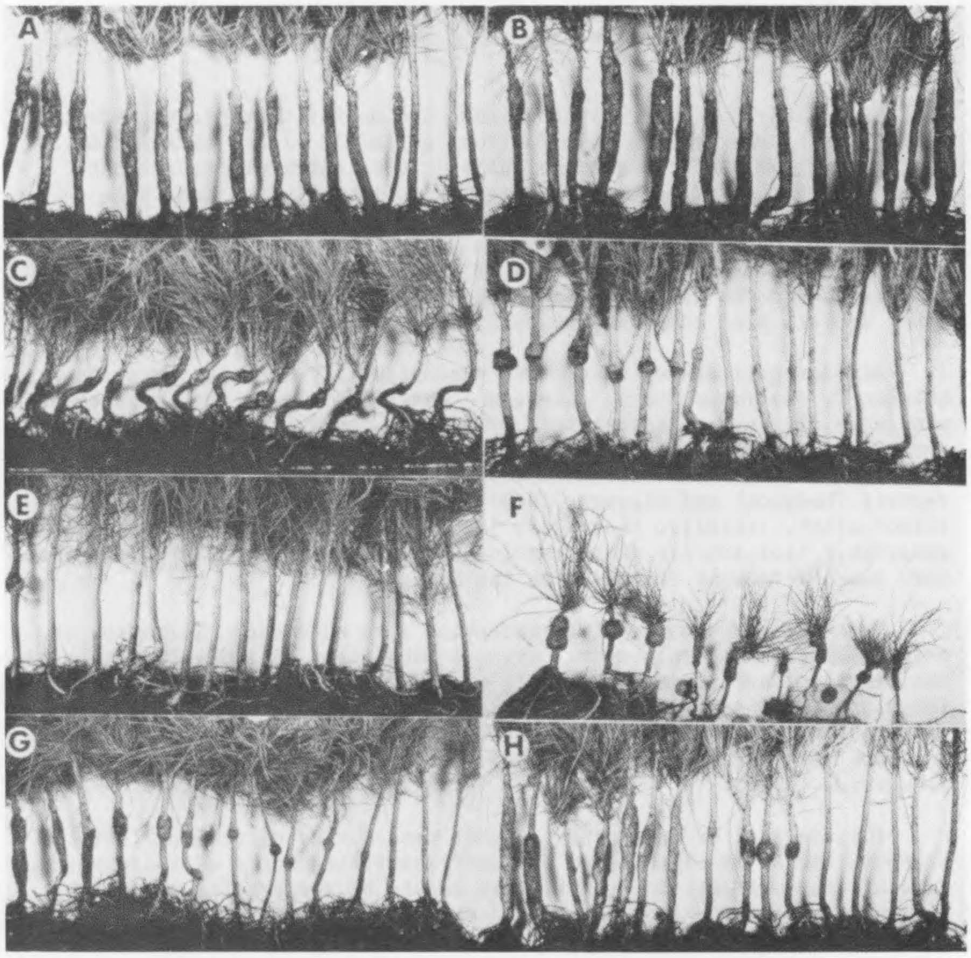


Figure 3. Gall formation at 12 months following pine inoculations with various isolates of *Cronartium:* (A) slash pine and (B) loblolly pine inoculated with *C. fusiforme* isolate No. 1; (C) shortleaf pine and (D) loblolly pine inoculated with *C. quercuum* Mississippi isolate No. 1; (E) slash pine inoculated with *C. quercuum* Mississippi isolate No. 2; (F) jack pine inoculated with *C. quercuum* Wisconsin isolate No. 1; (G) sand pine and (H) loblolly pine inoculated with *C. quercuum* North Carolina isolate No. 2.

DISCUSSION

From their different effects on the 5 species of pine, we believe that these three geographic sources of *C. quercuum* are distinct pathogenic races. The Wisconsin source was pathogenic to slash and jack pine; the North Carolina source was pathogenic to loblolly and sand pine; and the Mississippi source was pathogenic to slash, loblolly, shortleaf, and, to a lesser extent, jack pine. It is probable that further studies would reveal other pathogenic races of *C. quercuum*. Recently, pathogenic variability has also been observed in *C. fusiforme* (Snow, Powers, and Kais, 1969).

This study has generally confirmed the belief that plants infected with *C. fusiforme* tend to form fusiform galls and plants infected with *C. quercuum* tend to form globose galls. It is difficult to account for the formation of both types of galls on loblolly and sand pine inoculated with the one North Carolina isolate of *C. quercuum*. The plant response may be attributable to variability of the isolate or to variability within the two species of pine. Variability within the isolate may be the better explanation, since galls resulting from all other isolate-pine inoculations were uniform in shape.

Besides gall shape, host plant susceptibility definitely varies between *C. fusiforme* and *C. quercuum*. While shortleaf, jack, and sand pine were all very resistant to *C. fusiforme*, they were susceptible in some degree to one or more of the isolates of *C. quercuum*. When data for all our *C. quercuum* isolates are combined, they agree with past reports (Hedgcock and Siggers, 1949) in showing that *C. quercuum* can infect slash, loblolly, shortleaf, jack, and sand pine. But when the geographic isolates are evaluated individually, it becomes apparent that they cause different reactions on the hosts.

Two types of recovery from infection were observed: formation of primary symptoms (purple spots) without subsequent gall development, and the disappearance of definite galls on infected plants. All of the inoculated plants developed primary symptoms, an indication that the inoculation technique was very efficient. The recovery of plants from fusiform rust infection has been previously reported (Snow, Jewell, and Eleuterius, 1963).

The findings of this study suggest two courses of action. First, criteria should be established for differentiating races of these rusts. Second, tree breeders and geneticists should be prepared to cope with the problems arising from pathogenic variability in *Cronartium* species.

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FLOOR DISCUSSION

Panel leader Schütt withheld discussion of this paper until after the closely related paper by Dr. Powers, immediately following.

TESTING FOR PATHOGENIC VARIABILITY WITHIN *CRONARTIUM FUSIFORME* AND *C. QUERCUUM*

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ABSTRACT

The pathogenic variability of *Cronartium fusiforme* and *C. quercuum* was investigated using aeciospore collections from different pine hosts and different geographic locations. Each collection was used to inoculate northern red oaks. Telia formed on these oak leaves were used to inoculate 4- to 6-week-old seedlings of 16 species of hard pines. Between 300 and 400 seedlings of each pine species were inoculated with each rust collection. After growing for 7 to 9 months in a greenhouse, these seedlings were examined for stem galls.

Four collections of *C. fusiforme* produced relatively uniform infection response on the 16 pine species. Infection averaged almost 80 percent on very susceptible species, such as Jefferey, Monterey, South Florida slash, and ponderosa pine. Loblolly, slash, and Austrian pine had intermediate infection percentages, ranging from 35 to 50 percent. A large number of species were highly resistant, including such southern species as pond, sand, and spruce pine.

The two collections of *C. quercuum*, one from jack and one from Virginia pine, produced contrasting infection results on several of the pine species tested. The Virginia pine collection produced galls on 43 percent of the Virginia pine seedlings and none on the jack pine, and the jack pine collection produced 70 percent infection on jack pine but none on Virginia pine. This demonstrated the existence of distinct physiologic races of this organism.

Breeding for rust resistance requires an understanding of the pathogenic capabilities of the causal fungi. In the South, the most important pathogen of planted slash (*Pinus elliottii* var. *elliottii* Engelm.) and loblolly (*Pinus taeda* L.) pine is the fusiform rust fungus *Cronartium fusiforme* Hedgc. and Hunt ex Cumm. This fungus, which produces spindle-shaped galls on branches and stems, causes extensive damage to nursery seedlings, young plantations, and seed orchards (Verrall, 1958; Campbell, Darby, and Barber, 1962). Another pine-oak rust fungus, the eastern gall rust (*C. quercuum* (Berk.) Miyabe ex Shirai), also occurs in this same geographic area because the range of one of its primary hosts, shortleaf pine (*Pinus echinata* Mill.), extends southward almost to the Gulf of

Mexico and eastward to the Atlantic coast (Anderson, 1963). In contrast to fusiform rust, this fungus causes globose or cerebroid galls on its pine hosts. It also differs from fusiform rust in that it causes only slight damage to the southern pines that it infects, such as shortleaf, sand (*P. Clausa* (Chapm.) Vasey), and Virginia (*P. virginiana* Mill.). However, these two rust fungi are nearly indistinguishable on their oak alternate hosts.

Although there is information about the pine host ranges of these two fungi (Hedgcock and Siggers, 1949), very little is known about the pathogenic variability inherent within each population. The objective of this study was, therefore, to evaluate the variability of several collections of both these fungi as expressed by infection on a range of hard pine species.

Four aeciospore collections of *C. fusiforme* from three geographic areas of the South and two aeciospore collections of *C. quercuum*, one from the Southeast and one from the North Central states, were used (Table 1). Each rust collection was made from a single gall. Inoculation with one rust collection was completed before work with the next rust began, in order to prevent contamination. The aeciospores were used to inoculate northern red oaks (*Quercus rubra* L.). Telia that formed on the oak leaves were suspended for 48 hours over 4- to 6-week-old pine seedlings in a mist chamber at approximately 70°F. Sixteen species of hard pine, including both native and exotic species, were inoculated. Between 300 and 400 seedlings of each species were inoculated with each rust collection. The inoculated seedlings were grown for 7 to 9 months in a greenhouse and then were examined for stem galls.

Table 1. Collections of rust used in pathogenic variability study

Culture number	Species	Geographic source	Pine host
631	*C. fusiforme*	Upper Piedmont South Carolina	loblolly
632	*C. fusiforme*	Upper Piedmont South Carolina	loblolly
645	*C. fusiforme*	Lower Coastal Plain South Carolina	loblolly
WSP1	*C. fusiforme*	Mississippi (albino strain)	slash
648	*C. quercuum*	Western North Carolina	Virginia
671	*C. quercuum*	Minnesota	jack

The four collections of *C. fusiforme* produced relatively uniform infection responses on the 16 pine species (Table 2). On very susceptible species, such as Jefferey, Monterey, South Florida slash, and ponderosa pine, infections averaged almost 80%. This indicates that all species were exposed to relatively high concentrations of inoculum under conditions conducive to infection. Even under these optimum conditions, some species, such as loblolly, slash, and Austrian pine, had intermediate infection ranging from 35 to 50%. Nine of the species were essentially resistant. This latter group included such southern species as pond, sand, and spruce pine.

These results agree generally with the earlier work by Hedgcock and Siggers (1949). In comparison with Hedgcock and Siggers data, our loblolly infection was lower, the slash pine higher, and Jefferey, ponderosa, and Monterey considerably higher. One of the most interesting differences relates to infection on pond pine. Hedgcock and Siggers reported that pond pine, with 38% infection, was almost as susceptible as slash pine (41% infection). Only one collection in our study, #645 from coastal South Carolina where pond pine is native, produced an appreciable amount of infection (7%). This is considerably less than Hedgcock and Siggers reported and may possibly indicate pathogenic variability on the part of the fungus, difference in resistance on the part of the host, or simply a difference in inoculation techniques.

Kais and Snow[1] indicated some differences in levels of pathogenicity between collections of *C. fusiforme* on different strains of slash pine. Overall, however, *C. fusiforme* seems relatively uniform in its pathogenicity.

The two collections of *C. quercuum*, one from jack and one from Virginia pine, produced contrasting infection results on several of the pine species tested. The Virginia pine collection (#648) produced galls on 43% of the Virginia pine seedlings and on 1% of the jack pine; the jack pine collection (#671) produced 70% infection on jack pine and none on Virginia pine. This demonstrates the existence of distinct physiologic races of this organism. The differential reactions of these pine hosts are of essentially the same magnitude as those of the wheat rust differentials used to distinguish between the numerous races of *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and Henn. The 2 pine hosts involved are, of course, different species. In the case of wheat stem rust, 5 different species of *Triticum* make up the differential varieties, so again the situation is comparable.

In addition to the differential responses on the jack and Virginia pine, there were several sharp differences in the amount of infection on some other species. Sand pine, for example, was quite susceptible (54%) to collection #648, but was highly resistant (1%) to collection #671. Loblolly pine was only slightly susceptible (20%) to collection #648 and highly resistant (1%) to #671. Slash pine was also slightly susceptible to collection #648 (17%), but quite susceptible (54%) to #671. However, the infections on slash pine caused by both *C. quercuum* collections were atypical, producing a very small, round gall with copious resinosis.

[1] *See Kais and Snow, these proceedings.*

Table 2. Amount of infection on 16 species of hard pines resulting from inoculations with 6 rust collections

Pine species	*Cronartium fusiforme*[a]				*Cronartium quercuum*[b]	
	631	632	645	WSP1	648	671
	%	%	%	%	%	%
Loblolly	28	45	35	27	20	1
Slash	53	42	58	48	17	54
South Florida Slash	82	82	85	76	85	85
Shortleaf	1	4	0	4	5	0
Virginia	2	1	0	2	43	0
Spruce	--	0	0	0	3	Trace
Pond	0	1	7	1	1	0
Sand	3	0	0	0	54	1
Jack	1	0	0	0	1	70
Pitch	0	1	0	0	3	0
Ponderosa	77	78	74	91	63	75
Jefferey	76	81	65	76	78	86
Monterey	81	79	68	79	78	89
Red	0	0	0	0	0	0
Austrain	39	39	39	36	52	73
Scots	12	0	1	1	--	27

[a] Cultures 631, 632, and 645 from loblolly pine; culture WSP1 from slash pine.

[b] Culture 648 from Virginia pine; culture 671 from jack pine.

Comparisons between these infection data with *C. quercuum* and those of Hedgcock and Siggers with the same organism are difficult to make because Hedgcock and Siggers did not always indicate the original host source of the collections. There are also differences in inoculation techniques. The majority of Hedgcock and Siggers inoculations were made by inserting telia into slits in the phloem of young shoots. It is not known just what effect this radical method of inoculation might have on a species with borderline resistance.

The differences between the two collections of *C. quercuum* demonstrated by our data (Table 2) are supported by similar findings reported by Kais and Snow in these proceedings. Therefore, it can be said that distinct pathogenic races, using the term in the classic sense, exist within the overall population of *C. quercuum*.

It is possible that *C. fusiforme* may be less variable in pathogenicity than *C. quercuum*. *C. quercuum* has a much wider natural range, covering most of the eastern half of the country and it is common on a relatively wide range of pine hosts in the North and South. *C. fusiforme* is found in a much more limited geographic area in the South, and has only two primary hosts, loblolly and slash pine. Therefore, it would be expected that the chances for the development of pathogenic differences would be much greater in the case of *C. quercuum*, although the possibility of such variability should not be ruled out for *C. fusiforme*.

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FLOOR DISCUSSION

(Discussion here also covers the previous paper by Kais and Snow.)

POPE: Dr. Powers, do you think that what we are calling races here in the pines is the same as what people working with stem rusts of wheat are calling races, in light of the fact that here we are using a number of pine species whereas with the wheat rust, they are talking about varieties?

POWERS: Of course, there are some differences, but as I mentioned, they do have five different species involved in their standard wheat stem rust differentials. Within the standard differentials you have *Triticum vulgare* and a group of other wheat species, so essentially they are trying to determine differences between their different physiologic races with different host species just as we have the different pine species. There is another point to be mentioned here and that is that we do not have anything comparable to their situation going from a zero fleck all the way up to a four infection type. We are simply talking

about gall formation or lack of gall formation. Dr. Dwinell who is here with me from Athens, Georgia, has done some very interesting work with the differences between *C. quercuum* and *C. fusiforme*, especially on the infection type on the oak alternate host, and it may be that we are getting to the point you are making; something comparable with the wheat rust infection types. Maybe we should look on the oak side of the picture.

KAIS: I would like to make a comment here. I have studied isolates of *Cronartium fusiforme* collected from different geographic areas and have concluded that pathogenic variability occurs between geographic sources of the fungus. We have detected these differences on a single progeny of slash pine.

COWLING: I'd like to ask both of the speakers about a suggestion Dr. Callaham made during the coffee break. He suggested that a central facility be formed to evaluate the progenies and selections of all of the tree improvement programs of the south. Supposing that facility were created, what would be your recommendations so far as inoculum is concerned? Would you use both *Cronartium fusiforme* and *C. quercuum* or would you use mixed inoculum or what would be your recommendation?

POWERS: I would suggest a specific known culture of *C. fusiforme*. And if necessary let Dr. Dwinell check it out with his black oak response to make sure you had what you thought you had, and use that to screen routinely. We will undoubtedly continue to screen not on a mass basis, but on a limited research basis with other specific isolates. For overall screening, I think I'd select one known isolate of *C. fusiforme*, because the *C. quercuum* really isn't the problem that *C. fusiforme* is.

KAIS: I agree. For economic reasons, we should use *C. fusiforme* since *C. quercuum* is relatively unimportant.

CALLAHAM: Dr. Powers, you may be in conflict with what Kais just said. Did you suggest using only a single isolate or a single geographic source when he already has evidence of geographic variation in the species and in its responses? Should we not start considering the interactions among provenances of parasite and provenances of host?

POWERS: Naturally, if you have two different races within *C. fusiforme*, you need to screen with both.

CALLAHAM: Do you have evidence of races of the rust within the south, for example?

KAIS: We have, yes, and it will be published.

COWLING: Why don't you use a mixed inoculum?

POWERS: I imagine you might cover up some possible sources of resistance.

COWLING: Would you not also avoid the mistake of having certain progenies that are actually susceptible to fusiform rust appear to be resistant?

DINUS: The nature of the data of which Kais is speaking is available in the recent Southern Conference on Forest Tree Improvement. Also, I would like to make a plea that a much more detailed investigation of this phenomenon be undertaken before any real suggestion is made as to what to do about it, or before anybody actually makes a move toward trying to set up a central testing facility.

KINLOCH: It seems to me that you have got two distinct problems here. If your objective is screening for production of resistant stock to plant over a wide range of the host, then it seems desirable to screen against the maximum genetic variation of the rust that you're likely to encounter. Now, if you get host resistance after that you're in pretty good shape for production. It does not answer whether racial variation is present, however, when you're putting all the potential races in an area into one inoculation. If you want to detect and prove the existence of races you've got to start with genetically uniform inoculum. If you're looking just for resistance in the host to any and all potential races then you get as many sources of inoculum together as you can. The two problems are separate.

POWERS: Dr. Kinloch, this gets back to Dr. Cowling's question. I think you could do it either way, depending on your objective. I still do not think, however, that I would mix *C. quercuum* and *C. fusiforme*. I think I'd stay with *C. fusiforme*.

COWLING: I meant a mixed source of inoculum of *C. fusiforme*.

POWERS: Oh, yes, possibly so. In any event I think I would not, at this stage, bother with *C. quercuum*.

CAMPANA: I have the impression that *C. fusiforme* is much more devastating in speed of killing the stem than is *C. quercuum* and I would like to ask either one of the two speakers if this is an accurate impression, and if so, is this difference in pathogenicity related to the nature of the gall, and any histological difference between tissues in the gall.

POWERS: I think this is quite true. *C. fusiforme* is a much more lethal rust. If you're going to get into the anatomy, could I refer you to Dr. Frederick Jewell? He has done a great deal of work on the subject.

JEWELL: The main tissue differences that show up are in the phloem. With *C. fusiforme*, the phloem is much more disrupted and you don't get as many sieve cells formed. With *C. quercuum*, you have a normal complement. They are bent out of shape, true, but the transpiration stream is not broken as it is in the slash pine with *C. fusiforme*. It's really disturbed because they get all mixed up with parenchyma cells. While I'm here, I would like to bring out another point. The question as to the specificity of these two fungi has been raised many times. In other words, do we have two separate species of fungi here or do we have one and a variation of one? Dr. Powers' data showed they infect the same trees, and I was just wondering if possibly we do have a race of *C. quercuum* and that happens to be *C. fusiforme*. Bat that around for awhile.

POWERS: We could spend half the day on that, I think, Dr. Jewell. Arthur, in his manual of the rusts, did lump all of these pine-oak rusts together, and this thing has been batted back and forth many times. We'd have to have a discussion session on this alone.

VEGETATIVE PROPAGATION EXPERIMENTS IN WHITE PINE

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ABSTRACT

Vegetative propagation is a vital tool for defining genetics of resistance and pathogenicity. Rooting of white pine cuttings and needle fascicles was attempted. Results showed that (1) cuttings and needle fascicles of *P. griffithii* x *strobus* rooted better than those of *P. strobus*, (2) rooting ability of *P. strobus* did not decrease significantly up to the age of 10 years, (3) no significant differences were found in the rooting between cuttings and needle fascicles, (4) cuttings and needle fascicles rooted either in plastic tubes or in flats, (5) cuttings planted in tubes developed an evenly distributed and balanced root system in contrast to the unilateral roots developed on cuttings in flats, (6) cuttings planted in tubes showed a better survival than those planted in flats, and (7) coarse sand with a bottom layer of white pine humus was a superior rooting medium to a mixture of sand and humus.

The experiments also gave indications that (1) differences in rooting ability existed between different white pine species and their hybrids, (2) differences in rooting ability existed among populations of the same species or hybrid, (3) within population variation in rooting ability existed, and (4) within population variation in rooting ability was more pronounced with age.

INTRODUCTION

The white pine vegetative propagation trials were initiated to exploit more accurate means of blister rust resistance testing and to prevent the loss of genetic gain achieved in the selection of blister rust-resistant trees. Vegetative propagation provides full utilization of the resistant trees and a shortcut in white pine improvement work.

Farrar and Grace (1940, 1942) made observations on the influence of time of cutting collection on rooting. They obtained better results with *Pinus strobus* L. cuttings collected and planted in late August than with those taken in the spring.

Thimann and Delisle (1939) studied rooting differences of cuttings taken from various parts of the crown. They found that cuttings taken from lateral branches rooted consistently better than those taken from

terminal shoots and grew as vertical as the terminals. Cuttings taken from the basal part of the crown rooted better than those taken from the apical part.

Several authors have studied the influence of ortet age on rooting. Thimann and Delisle (1939) found that cuttings taken from 1- to 3-year-old *P. strobus* rooted easily, and that rooting ability of older trees decreased. Cuttings taken from mature trees were difficult to root even with auxin treatments. Snow (1940) found no significant decrease in the rooting of cuttings taken from *P. strobus* trees 15 years of age or younger. Doran, Holdsworth and Rhodes (1940) successfully rooted cuttings taken from 30-year-old eastern white pines. Patton and Riker (1958a) had far less success in rooting cuttings taken from trees over 10 years of age.

Large individual variation in rooting ability was reported by Snow (1940) and Patton and Riker (1958b). They noticed, furthermore, a fluctuation in rooting ability of the same clones in different years.

Thomas and Riker (1950) found it difficult to lift and transplant rooted cuttings of eastern white pine because of their unilateral and unbalanced root system. However, once the rooted cuttings started to grow, they developed normally. Patton and Riker (1954) found no significant differences in the survival and growth of seedlings and rooted cuttings after 12 years.

Needle fascicles produce a large number of propagules. Thimann and Delisle (1942) rooted needle fascicles of eastern white pine. Mergen and Simpson (1964), experimenting with hard pine needle fascicles, found a sharp decrease in rooting ability with ortet age and had difficulty in obtaining rooted needle fascicles that would grow. However, once a rooted fascicle started to grow, it developed into a normal tree. Recently, Hoff and McDonald (1968) rooted western white pine (*Pinus monticola* Dougl.) needle fascicles. Only the needles with fascicular buds produced shoot growth. Bud formation can be induced in needle fascicles of *P. strobus* by pruning the terminals in early summer (C. Heimburger, *unpublished data*).

MATERIALS AND METHODS

During the winter of 1967 and spring of 1968, a series of experiments dealing with the vegetative propagation of white pines were initiated. All trials were established with propagules taken from lateral branches in the basal part of the crown. The propagules were dipped in 50% captan powder[1] and planted in coarse acid sand (except in the experiment on media) either in tubes or in rooting beds.

Slit tubes, made of polystyrene, were 3/4 inch in diameter and 3 inches long (described by McLean, 1959). These tubes were arranged in 16-x-8-inch wooden flats which were covered with transparent polyethylene and kept shaded in a greenhouse. The greenhouse temperature varied from 50° to 100°F, and the humidity was not controlled.

[1] *50% captan is orthocide 50, a N-trichloromethylmercapto - 4-cyclohexene - 1,2 - dicarbomixide compound.*

The rooting beds were covered with aluminum painted polyethylene sheets. Light intensity under the plastic was only 5 to 10% of that in the open and the temperature generally ranged from 60° to 90°F, but reached as high as 105°F.

The final tally was taken 5 months after planting. Chi-square tests were calculated for the percentage of rooted propagules. The influences of collection date, ortet age, propagule type, planting containers, and media were studied. In addition our efforts included a preliminary investigation of genetic influences.

INFLUENCE OF COLLECTION DATES

Rooting tests were established in December, January and March using cuttings and needle fascicles without buds. The propagules were taken from trees in a 5-year-old population of *P. strobus* and in 5- and 15-year-old populations of *Pinus griffithii* McClelland (syn. *P. wallichiana* A.B. Jacks.) x *strobus*. In each test 20 propagules per population were planted in 3 replications.

INFLUENCE OF ORTET AGE

Three comparisons were made to study the effect of ortet age. In the first, results obtained from all the *P. griffithii* x *strobus* propagules in the above experiment were examined on the basis of ortet age rather than collection and planting date. The second analysis used cuttings taken in May 1968 from ortets belonging to 2-, 5- and 15-year-old populations of *P. griffithii* x *strobus*. The third test utilized 5- and 10-year-old and regrafted mature *P. strobus* ortets. These cuttings were also taken in May 1968.

INFLUENCE OF TYPE OF PROPAGULE

Cuttings and needle fascicles used to study the influence of collection date and ortet age on rooting were also used in this portion of the investigation.

INFLUENCE OF TUBES AND ROOTING BEDS

This experiment compared cuttings taken from *P. strobus* and *P. griffithii* x *strobus* ortets 5, 10, and 15 years old. The regrafted mature *P. strobus* ortets were also included. The cuttings in tubes were identical to those described in the collection date experiment; the cuttings in rooting beds to those described in the second and third analyses of the ortet age experiment.

INFLUENCE OF MEDIA

In May 1968 cuttings from a 5-year-old population of *P. strobus* were planted in rooting beds in the following soil media: (1) nursery soil characterized as a dark brown calcareous clay loam; (2) a soil complex made up of a top layer of coarse acid sand (4 in.) and a bottom layer of white pine humus (1 in.); and (3) a 1:1 mixture of coarse acid

sand and white pine humus. Single plots, containing 21 cuttings, were planted in 4 replications.

VARIATION IN ROOTING WITHIN AND BETWEEN POPULATIONS

The within population variation in rooting was studied on cuttings planted in rooting beds in May 1968. The cuttings were taken from several trees from 5- and 10-year-old populations of *P. strobus* and from 2-, 5- and 15-year-old populations of *P. griffithii* x *strobus*. Twenty-six cuttings from all except the 2-year-old tree were planted in 2 replications.

The between population variation in rooting was studied on two populations of *P. griffithii* x *strobus*. Each population was represented by two 5-year-old trees. Again, 26 cuttings were taken from each tree and planted in 2 replications in rooting beds in May 1968.

Variation of rooting ability of cuttings obtained from *P. strobus* and *P. griffithii* x *strobus* ortets was determined for the 5-year-old populations just described.

RESULTS

The December, January and March collection dates showed no significant differences in rooting of cuttings. Needle fascicles collected and planted in January and March rooted significantly better than those planted in December (Table 1).

Table 1. Rooting of *P. strobus* and *P. griffithii* x *strobus* propagules collected at different times: ortets 5 and 15 years old

Propagule type	Month of collection: December No. rooted	December % rooted	January No. rooted	January % rooted	March No. rooted	March % rooted
Cuttings	7	23.3	6	20.0	8	26.7
Needle fascicles	5	16.7	12	40.0	11	36.2

Cuttings: $\chi^2 = 0.96$ d.f. = 2

Needle fascicles: $\chi^2 = 10.19^{**}$[a] d.f. = 2

[a] ** significant at the 1% level

Significant differences in rooting appeared between the propagules taken from trees of different age. Although rooting decreased with age, no difference was observed with propagules taken from trees 10 years of age or younger (Tables 2, 3, 4).

Table 2. Rooting of *P. griffithii* x *strobus* propagules obtained from 5- and 15-year-old ortets: December, January, and March collections

Propagule type	Age of ortet: 5 years No. rooted	5 years % rooted	15 years No. rooted	15 years % rooted	d.f.	χ^2
Cuttings	11	36.7	2	6.7	1	20.84**[a]
Needle fascicles	12	40.0	6	20.0	1	6.67*

[a] * Significant at 5% level; ** Significant at 1% level.

Table 3. Rooting of *P. griffithii* x *strobus* cuttings obtained from 2-, 5-, and 15-year-old ortets: May collection

Ortet age	No. rooted	% rooted
2 years	30	23.0
5 years	45	34.6
15 years	13	10.0
$\chi^2 = 13.44$**[a]	d.f. = 2	

[a] ** Significant at 1% level

Table 4. Rooting of *P. strobus* cuttings obtained from 5- and 10-year-old and mature ortets: May collection

Ortet age	No. rooted	% rooted
5 years	15	11.5
10 years	14	11.0
Mature	1	0.8
$\chi^2 = 9.41$**[a]	d.f. = 2	

[a] ** Significant at 1% level

Rooting levels of cuttings and needle fascicles were not significantly different when propagule collection date was disregarded (Table 5). Needle fascicles taken from 15-year-old *P. griffithii* x *strobus* trees apparently rooted better than cuttings taken from the same trees, but the difference for 5-year-old ortets was not as great (Table 2).

Table 5. Rooting of *P. strobus* and *P. griffithii* x *strobus* cuttings and needle fascicles obtained from 5- and 15-year-old ortets: December, January, and March collections

Propagule type	No. rooted	% rooted
Cuttings	21	23.3
Needle fascicles	28	31.1
$\chi^2 = 1.12$	d.f. = 1	

Rooting of cuttings planted in tubes and in rooting beds were not significantly different. But, the cuttings survived better in tubes than in rooting beds (Table 6).

Table 6. Rooting and survival of *P. strobus* and *P. griffithii* x *strobus* cuttings planted in tubes and beds

Planting location	Ortet age	Collection time	Rooted No.	Rooted %	Survived No.	Survived %
Tubes	5 and 15	Dec., Jan., & Mar.	21	17.5	74	61.7
Beds	2, 5, 10 & 15 years & mature	May	88	13.5	143	22.0
$\chi^2 = 0.52$					$\chi^2 = 18.83^{***}$[a]	
d.f. = 1					d.f. = 1	

[a] *** Significant at the .1% level

The tubed cuttings developed a well balanced root system consisting of several vertically oriented roots (Fig. 1), while the cuttings in rooting beds developed an unbalanced root system consisting mainly of one long horizontal side root (Fig. 2).

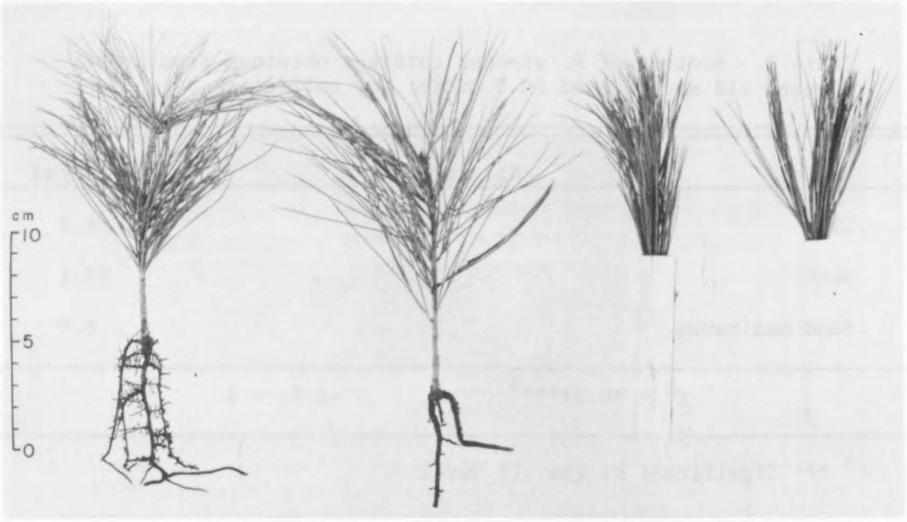


Figure 1. Rooted white pine cuttings with tube removed (left) and tube intact (right).

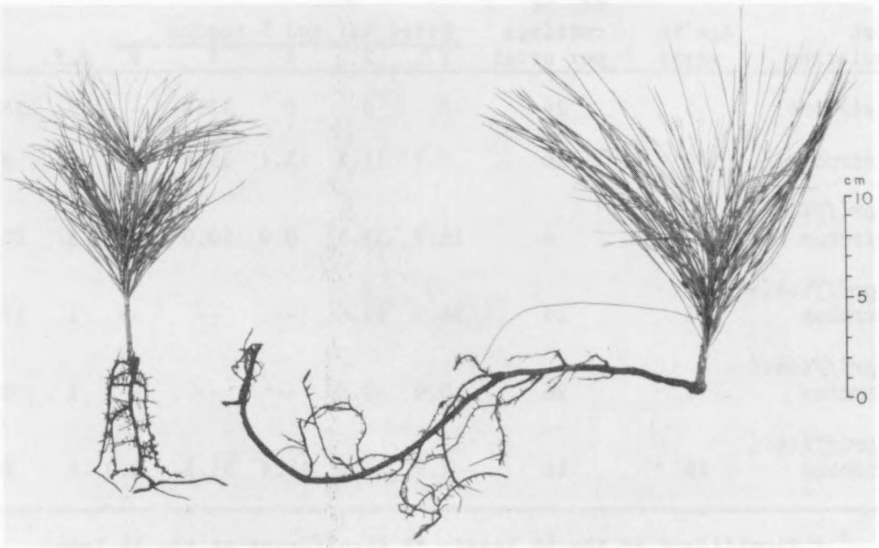


Figure 2. White pine cutting rooted in tube (left) and in rooting bed (right).

The rooting in coarse sand was significantly better than the rooting in clay loam or in a mixture of coarse sand and humus (Table 7).

Table 7. Rooting of *P. strobus* cuttings obtained from ortets 5 years old and planted in 3 media: May collection

Media	No. rooted	% rooted
Clay	5	6.0
Sand	53	63.1
Sand and humus	5	6.0
$\chi^2 = 86.84^{***}$[a]	d.f. = 2	

[a] *** Significant at the .1% level

The within population variation was significant in four cases but was not significant in two cases (Table 8).

Table 8. Variation of percentage rooting within ortets: May collection

Ortet population	Age in years	No. of cuttings per ortet	Ortet No. and % rooted 1	2	3	4	5	d.f.	χ^2
P. strobus	5	26	0	0	0	42.8	--	3	138.4**[a]
P. strobus	10	26	7.7	11.5	15.4	15.4	3.8	4	9.40*
P. griffithii x *strobus*	2	6	16.7	33.3	0.0	50.0	--	3	55.5**
P. griffithii x *strobus*	5	26	38.5	84.6	--	--	--	1	17.26**
P. griffithii x *strobus*	5	26	0.0	0.0	--	--	--	1	0.0
P. griffithii x *strobus*	15	26	7.7	15.4	15.4	11.5	0.0	4	6.59

[a] * Significant at the 5% level; ** Significant at the 1% level

The difference in rooting between the two *P. griffithii* x *strobus* populations of the same age was significant (Table 9). Likewise, *P. griffithii* x *strobus* rooted significantly better than *P. strobus* (Table 10).

Table 9. Variation of percentage rooting of *P. griffithii* x *strobus* cuttings obtained from 2 populations of 5-year-old ortets: May collection

Population	No. of cuttings	No. rooted	% rooted
1	52	0	0
2	52	32	61.1
$\chi^2 = 46.2^{***}$[a]		d.f. = 1	

[a] *** Significant at the .1% level

Table 10. Rooting of *P. strobus* and *P. griffithii* x *strobus* cuttings obtained from ortets 5 years old: May collection

Ortet species	No. rooted	% rooted
P. strobus	24	12.6
P. griffithii x *strobus*	68	35.8
$\chi^2 = 11.12^{**}$[a]	d.f. = 1	

[a] ** Significant at the 1% level

DISCUSSION

Some of these experiments confirmed results obtained in other studies; for example, the information on rooting by using various rooting media (Nienstaedt, *et al.*, 1958) and on age influence in rooting (Delisle, 1954). In the *P. strobus* tests, rooting ability did not decrease up to an age of 10 years. This should allow enough time to test for blister rust resistance prior and parallel to vegetative propagation.

We did not find differences in the rooting of cuttings and needle fascicles (Table 5). This means that the rooting of needle fascicles would be advantageous as it offers possibilities for rapid mass propagation. However, it seems that only the needles with fascicular buds are able to develop into a normal plant. The induction of fascicular buds by pruning the terminals should not present any problem. Hoff and McDonald (1968) successfully rooted needles with fascicular buds. If the rooting of such fascicles with buds is as easy as the rooting of those without buds, then this method would become a very valuable means of vegetative propagation in white pines. Roots developed on needle fascicles are shown in Fig. 3.

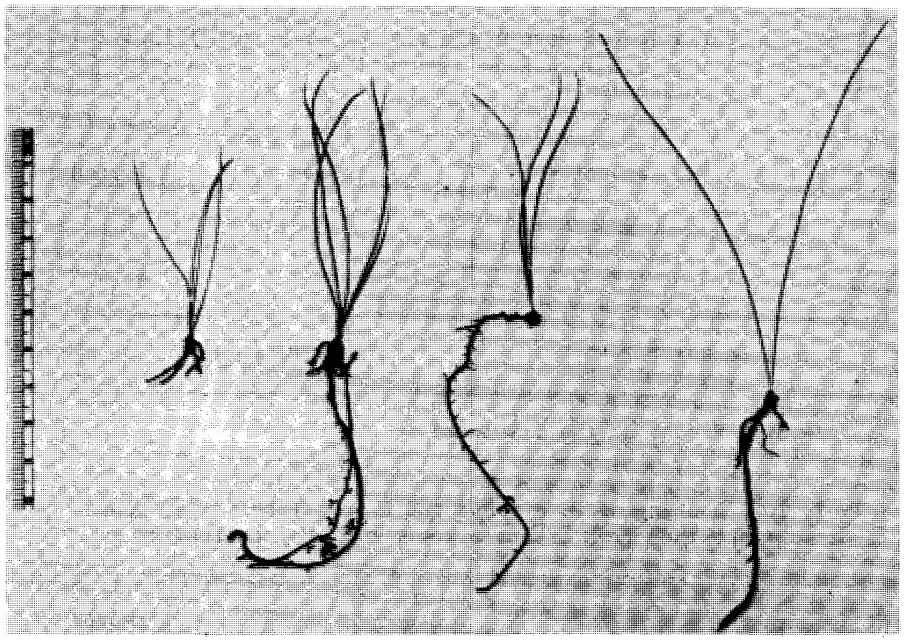


Figure 3. Rooted white pine needle fascicles.

Cuttings rooted in small plastic containers are a very useful method of vegetative propagation. The cuttings planted in tubes showed better survival and root development. The better survival of cuttings may be attributed to the isolation of parasites and saprophytes which destroy the weakened cuttings. While the root system of cuttings planted in open flats or rooting beds is usually unbalanced, consisting of one long horizontal side-root, the cuttings rooted in tubes developed a well-balanced root system consisting of several vertically oriented roots (Figs. 1 and 2). This is one of the greatest advantages of rooting in tubes. Other advantages of this method are that the tubes require less space and that the cuttings and needle fascicles planted in tubes can be checked, moved or outplanted anytime without risk of breaking the roots or losing the plant.

Significant within population differences in rooting were found in the majority of cases. Patton and Riker (1958b) also found distinct differences in rooting ability of white pine clones. Establishing individuals with superior rooting ability could be of great importance for the development of white pine clones.

Significant differences in rooting ability were found between the two *P. griffithii* x *strobus* populations of the same age. A significant variation in rooting ability apparently existed between the rest of the *P. griffithii* x *strobus* populations, as well as between the *P. strobus* populations in the experiments. A statistical comparison of their rooting ability could not be made because of the differences in age which might also have been an influencing factor.

Not much is known about the rooting ability of different white pine species and their interspecific hybrids. This problem is worth

investigating. In the described tests, *P. griffithii* x *strobus* was superior to *P. strobus*. The better rooting ability of the hybrid may be inherited from *P. griffithii* or it may be a quality of this interspecific hybrid, characterized by hybrid vigor.

The between species variation in rooting ability of white pines and the between and within population variation in the rooting ability of eastern white pine are now under investigation. I expect to obtain information which will enable me to choose species, hybrids, populations and individuals of superior rooting ability.

SUMMARY

The December, January and March planting dates showed no significant differences. Rooting decreased with age, but no difference was noted with propagules taken from trees up to 10 years of age. Needle fascicles without buds rooted as well as cuttings. Propagules developed an evenly distributed and balanced root system when planted in slit plastic tubes.

Differences in rooting existed within and between populations. The cuttings of *P. griffithii* x *strobus* rooted better than those of *P. strobus*. Future experiments may provide more information on variation in rooting ability.

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FLOOR DISCUSSION

Due to time being limited in this panel, this paper was offered only in abstract form and there was no discussion.

STEM RUSTS OF CONIFERS AND THE BALANCE OF NATURE

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ABSTRACT

"Total resistance" of western white pine to blister rust is a composite of independent mechanisms. The mechanisms that have been defined are all inherited in a simple Mendelian manner. Certain mechanisms not yet defined may be inherited in a quantitative manner.

There are at least two virulent races of *Cronartium ribicola* plus a third race that appears only to modify the action of the virulent races.

Several accepted methods for production of new resistant populations are discussed in light of blister rust resistant white pines. A new scheme, based upon the balance of natural host:parasite systems, is proposed.

A list of questions concerning the biological aspects of the white pine:blister rust system is presented. Many of these questions must be answered before a program designed to mass produce resistant seedlings can proceed with maximum likelihood of success.

INTRODUCTION

This symposium has drawn attention to the long period of time involved in breeding for disease resistance in forest trees. Breeding white pines (mainly *Pinus strobus* L. and *P. monticola* Dougl.) for resistance to the white pine blister rust fungus, *Cronartium ribicola* J.C. Fisch. ex Rabenh., has already spanned 30 years. Much progress can be noted, but we are just beginning to understand the meaning of "resistance."

The first objectives of these early programs were to demonstrate genetically controlled resistance and to develop "interim" stocks having a useful level of resistance. There is little doubt that such resistance is present in wild populations of *P. strobus* and *P. monticola* (Riker *et al.*, 1943; Patton and Riker, 1958; Bingham, Squillace, and Duffield, 1953; Bingham, Squillace and Wright, 1960; Bingham *et al.*, 1969).

Comparatively little time has been available to study the fundamental biological aspects of this disease, and it is precisely such fundamental knowledge that is required for the production of a new

population containing adequate levels of long-lasting resistance. Thus, the tree breeder's problem lies in gaining enough understanding of resistance so that a correct decision can be made before years of investment have accumulated on a product destined for probable failure.

The purposes of this paper are: (1) to summarize the factors for resistance observed in blister rust-resistant western white pine (*P. monticola*); (2) to discuss recently proposed agronomic schemes for incorporating factors for resistance into a long-lasting product; (3) to present an approach to the problem of breeding blister rust-resistant western white pine based on the natural models of resistance available in many tree-rust systems; and (4) to outline the specific knowledge required to implement a breeding program aimed at producing blister rust-resistant western white pine.

PHILOSOPHY OF DISEASE RESISTANCE BREEDING

In recent years decided changes have occurred in the philosophy of breeding for disease resistance in plants (van der Plank, 1963, 1968, 1969; Zadoks[1]). These changes place emphasis upon long-lasting but undramatic uniform (also termed general, horizontal, and field) resistance and tolerance instead of the more dramatic differential or specific resistance. This change of emphasis came about because of the general, if not universal, breakdown of differential or specific resistance by virulent races of the pathogen.

Lessons learned by the breeders of agronomic crops are important for forest tree breeders. The 120-year rotation used in the past by the Forest Service for western white pine in northern Idaho might be reduced to 60 years on the better sites, but this rotation would still require the use of resistance genes with a life expectancy of at least 30 to 40 years. This is far beyond the average life span of differential resistance genes in annual crop plants.

Presently, long-lasting uniform resistance, together with tolerance, appears to offer the surest path of success. This should lead to the concomitant survival of all members of the system. In other words, we must learn to live with the pathogen. Our first objective should be to produce new populations of white pines that have at least a degree of resistance necessary to make their culture profitable.

THE DISEASE CYCLE

The disease cycle of blister rust has been covered previously in this symposium by Dr. Patton, but its importance to the study of resistance is great enough to justify a summary. The fungus generally enters its pine host through stomata of the primary and secondary leaves, but entry through succulent stem tissues is also possible, at least under controlled conditions. Once in the leaf the fungus usually grows toward the stem via the vascular cylinder. Rapid spread in the living tissues of the stem produces the characteristic fusiform canker. Production of aeciospores takes place within the margins of the canker, and complete girdling of the main stem by the fungus finally results in death of or severe damage to the tree.

[1] *Paper presented in these proceedings.*

This disease cycle gives rise to a host-parasite system characterized by sequential resistance. In other words, mechanisms for resistance can be clearly separated by space and time. Such a situation provides an opportunity for controlled manipulation of the disease cycle. The result is to greatly simplify studies on factors for resistance and to make more efficient the incorporation of several types of resistance into one individual. For example, trees exhibiting resistance known to be based in the leaf could be tested for resistance based in the stem by direct inoculation of the stem with basidiospores, infected leaves, or by bark patch grafting.

RESISTANCE FACTORS IN THE WHITE PINES

The published reports of the mechanisms or factors for resistance were previously covered in this Symposium by Dr. Patton. A summary of these factors follows:

1. Lower needle lesion frequency on secondary needles in some *P. strobus* individuals. This was also observed in *P. monticola* by Bingham (1954).

2. Hypersensitivity in the foliage of *P. peuce* Griseb., *P. armandii* Franchet, and *P. monticola*.

3. Needle spots only. This includes individuals of *P. strobus*, *P. monticola*, and *P. wallichiana* A.B. Jacks. (syn. *P. griffithii* McClell.) that had needles infected with blister rust that did not subsequently produce cankers.

4. Corking-out of established cankers by the formation of a wound periderm. Observed in *P. strobus* and *P. monticola*.

5. Bark hypersensitivity in which the fungus is killed before it can enter the stem. This has been observed and reported in *P. strobus* and *P. monticola*.

At this Station, we have new data and have confirmed some older findings on the resistance of western white pine to blister rust as follows:

1. There are at least two different pathogenic races of *C. ribicola* with corresponding differential resistance genes in *P. monticola*.

2. One host-parasite interaction is indicated by the formation of a yellow needle lesion and host resistance in the secondary needles is inherited as a single recessive gene.

3. A second host-parasite interaction is indicated by the formation of a red needle lesion and host resistance in the secondary needles is inherited as a single dominant gene.

4. A third host-parasite interaction is indicated by the formation of a long yellow or yellow-red spot with green islands of epidermal tissue.

5. The needle lesion frequency trait may be controlled by a single nondominant gene. This work did not take into account races and thus the

data will be re-evaluated. However, it is clear that needle lesion frequency is a resistance factor within the red and yellow spot forming races.

6. A recessive gene controls the premature shedding of infected needles (McDonald, 1969).

7. A recessive gene controls a fungicidal reaction in the vicinity of the short shoot (McDonald, 1969).

8. Differential inhibitory compounds in the foliage may partially explain needle resistance.

9. Slow fungus growth exists in certain resistant plants (McDonald, 1969).

Resistance believed to be controlled by single dominant genes has been observed in *P. lambertiana* Dougl. and *P. monticola* (Barnes, *personal communication*) and in *P. lambertiana* (Kinloch, Parks, and Fowler, 1970).

ACQUISITION AND MAINTENANCE OF LONG-TERM RESISTANCE

Incorporating rust resistance genes into tree planting stock will require much knowledge, time, and money because of the long generation time (10 to 15 years in western white pine) and the problem of selecting those resistance genes that will assure a high percentage of surviving trees and thus a profitable crop.

Several methods being tested by breeders of agronomic crops aim at the production of highly resistant and long-lasting varieties. Which of these might be best suited for a long-lived, long-rotation plant like western white pine? Should tree breeders chance factors giving differential resistance, or should such types be dropped, and all efforts concentrated on uniform resistance and/or tolerance? The scheme chosen might determine the fate of the species as an economical crop.

CLASSICAL METHODS FOR INCORPORATING RESISTANCE INTO PLANTING STOCK

Agronomists have devised three general schemes in trying to meet the constant challenges to resistance made by a continually evolving rust fungus.

Scheme 1

In scheme 1 we assemble as many different types of differential resistance as possible, combining them in a "synthetic" variety before releasing it for planting stock (Harberd, 1964). Here, to successfully parasitize this synthetic variety, the pathogen must contain all the required virulence genes at the same time. The chance of their simultaneous occurrence by mutation and/or recombination is remote. The difficulty with this method, as pointed out by Harberd, is that varieties already present may contain some of the same factors for resistance thus providing a "bridge" across which the pathogen can reinvade at a faster than anticipated rate. Breeders may also inadvertently break up the synthetic variety while selecting for other traits. Both possibilities enable the pathogen to accumulate the needed virulence genes one or a

few at a time, until finally all factors for resistance are again neutralized.

Scheme 2

This scheme involves the formation of multilineal varieties, hybrids, or a large number of varieties, each with a separate factor for differential resistance. These are then released in one area where it is known that the complementary rust races are largely absent (Borlaug, 1959, 1965, 1966). This scheme requires a constant awareness of the frequency of the genes for virulence in the pathogen populations, and varieties have to be changed periodically before new epidemics arise.

Scheme 3

A third scheme utilizes uniform resistance, together with tolerance reactions, as a base upon which to build differential resistance (Hooker, 1967). Under this scheme the breeder has assurance of obtaining a merchantable crop even though certain of the differential types may be broken down. However, van der Plank (1963, 1968) strongly suggests that, because of the "vertifolia" effect (a loss of uniform resistance coupled with selection for genes controlling differential resistance), selection should be based solely on uniform resistance and/or tolerance reactions.

Of what value are these schemes in breeding blister rust resistance in western white pine? Scheme 1 could be useful since there are several factors for resistance in western white pine, some of which are controlled by single genes. These genes could be incorporated into a single variety that might withstand infection for many years. This is not likely, however, since the bridges are already present in the natural population and we can assume that these genes would have the same fate as most single, differential genes in the crop plants. On the other hand, if some of the new hypothesized races had a low level of fitness on the alternate host (*Ribes* spp.) the resistance genes complementary to them would have a much greater potential. Moreover, certain factors for resistance may have great stability because of certain features of the blister rust disease cycle in western white pine. That is, if the fungus can enter the stem under natural conditions (at least at low levels of infection), the fungus would be able to complete its life cycle by circumventing resistance factors in the needle. Together these conditions would mean: (1) selection for virulent races complementary to the factors for resistance located in the leaves would be decreased by allowing the original races (races presumably with higher levels of fitness) to complete their reproductive cycle; and (2) the resulting level of stem infection would be low enough to allow production of an adequate timber crop because direct stem infection seems to be rare and would probably tend to be located at the end of branches. This is where the largest amount of succulent stem tissue would be available.

Scheme 2 holds very little promise. The relatively long rotation of western white pine prevents the continued and rapid change of host genotypes. Nevertheless, this scheme could be used if the new hypothesized virulent races had low fitness on *Ribes* in comparison to the less complex races. This, coupled with a mixture of many factors for resistance throughout the host populations, could mean a profitable harvest.

Scheme 3 appears to represent the best chance for lasting success, especially when the disease cycle is considered. So far, two factors for resistance appear to fall into the uniform resistance category, i.e., needle lesion frequency and slow canker growth. We hope there are others. Because of the "vertifolia" effect, van der Plank (1963, 1968) warns against selecting for uniform and differential resistance types at the same time. The nature of the disease cycle of blister rust in western white pine helps to circumvent this problem. Since resistance is expressed sequentially at several sites separated by space and time, selection can be made for both types in the same individual. For example, on those trees that are susceptible to either the "yellow-spot" forming race or "red-spot" forming race, or both, selection could be made for needle lesion frequency. Later, selection could be made for the needle-spots-only traits followed by selection for corking-out, bark hypersensitivity, or slow canker growth by stem inoculation. Simultaneous selection for slow canker growth and the other bark reactions would be more difficult. Selection for the corking-out reaction could be made, however, since it is not often expressed until the canker is well established. Thus, fungus growth rate would have been evident.

It appears that scheme 3 could be used essentially as developed by the agronomic workers. However, we must remember that agronomic programs are designed to cope with short-lived, genetically homogenous, and unnatural (artificial or man-maintained) systems whereas most forestry programs must be designed to cope with long-lived, genetically heterogenous and natural (little or no influence by man) systems. This situation poses the question, "Who should the foresters emulate--the agronomist or 'Mother Nature'?" Maybe we can emulate both.

NATURAL MODELS OF STABLE RESISTANCE

For the sake of this discussion, let us take as fact the supposition that host-parasite systems are subject to evolutionary forces. Then, we should expect such systems to tend toward stability (Mode, 1958; Person, 1959, 1968; Person, Samborski, and Rohringer, 1962; van der Plank, 1960, 1963, 1968, 1969). It follows that in plant communities that have not been totally disrupted by man highly stable systems would evolve. Stable host-parasite systems are evident in many diseases of forest trees (van der Plank, 1960).

The degree of balance within a host-parasite system is determined by the amount of damage to the reproductive activities of both host and parasite, since evolution operates through the reproductive process. Furthermore, the system is composed of two separate genetic mechanisms and a prolonged imbalance can end in destruction of the system.

The North American hard pines and their corresponding indigenous rusts are excellent examples of stable or balanced host-parasite systems. In an extensive review of the literature on stem rusts, Peterson and Jewell (1968) could cite no examples of major imbalances (epidemics) in these natural systems. Although both reproductive and economic damage can at times be severe, the survival of the host-parasite system is secure since widespread infections appear to occur only when all requirements for infection are particularly favorable. A good example of a compatible relationship, at least at the individual level, has been reported by Peterson (1960). He often found live mycelium of *Peridermium harknessii* Moore that was at least 200 years old in stem sections of lodgepole pine (*P. contorta* Dougl.).

If we can assume that *C. ribicola* is native to Asia, then populations of *P. armandii, P. wallichiana, P. koraiensis* Sieb. and Zucc., and *P. sibirica* Du Tour, all moderately to highly resistant to *C. ribicola*, also appear to be excellent examples of balanced, native systems. Spaulding (1929, 1956) concluded that the fungus was native to eastern Siberia on the fairly resistant *P. sibirica*; but from his data the origin might well have been in the range of any of the even more resistant Asiatic white pines (especially *P. armandii, P. koraiensis*, and *P. wallichiana*). Also, the high resistance of *P. cembra* L. implicates the European Alps as another possible gene-center for white pine blister rust (Schellenberg, 1904; Gäumann, 1950; Fassi, 1960) but the published evidence assembled by Spaudling (1929) indicates that the entry of the rust into the *P. cembra* stands of the Alps was the termination of the advance of the rust across Europe.

Good examples of imbalance are the North American white pines-*C. ribicola* systems. These systems are obviously unbalanced in favor of the fungus. If this condition existed for long and if native populations of the white pines contained no resistance genes, the white pines would not survive within the range of the fungus. A lack of resistance in the American chestnut (*Castanea dentata* (Marsh.) Borkh.) to chestnut blight (caused by *Endothia parasitica* (Murr.) A. and A.) will likely result in the extinction of the host species.

BALANCED SYMBIOSIS

If the natural host-parasite systems are considered on the basis of population interaction, and if damage is measured by interference with reproductive processes, then we may be able to define the concept of natural systems in terms of an established concept. We suggest using symbiosis, realizing that this concept is generally restricted to interactions between individiauls. But for the lack of a more descriptive term, we wish to take the literal meaning--living together of dissimilar organisms--and extend it to include living together of *populations* of dissimilar organisms. We can now describe the natural system as being in a state of "balanced symbiosis" and define the two interacting species as symbionts.

Thus far we have considered only the biological balance of a system--that is, the ability of a species to survive. But man is primarily interested in the economic aspects of this balance. Therefore, he is concerned with loss in productivity expressed as direct mortality or cull. For instance, the damage of *C. fusiforme* Hedgc. & Hunt ex Cumm. on *P. taeda* L. (loblolly pine) and *P. elliottii* Engelm. (slash pine) is not biologically severe (the systems have survived) but the economic loss is quite high. However, for many of the pine and indigenous rust systems the economic loss is not great enough to justify a breeding program to increase rust resistance even though the loss in a particular year may be substantial (Peterson and Jewell, 1968; Fassi, 1960; Bakshi and Singh, 1967). Obviously a system such as the North American white pines-blister rust which is biologically out of balance in favor of the rust will show high economic losses.

CORRELATION OF FACTORS FOR RESISTANCE

Information on factors for resistance is still scanty but striking similarities occur within the pines in response to infection by the various rusts. Fewer lesions per unit area of infection court and slower fungus growth appear to be the most common factors so far observed. The needle-spots-only traits, either in secondary needles or primary leaves, also appear frequently. Prevention of penetration of secondary needles appears to occur throughout the hard pines and at times within the soft pines. Canker death has been reported for many of the soft and hard pines.

Admittedly this information is fragmentary. Even so, we are led to ask, "Have similar resistance factors evolved in the species of a genus that ward off diseases caused by related pathogens?" In other words, is there one set of factors for resistance that protect the pines from the stem rusts? While there may be one set of factors, different combinations may be found within the various host-parasite systems. However, exactly the same combination of factors for resistance may have evolved to protect closely related host species against a particular rust. If this is so, knowledge concerning one part of the total pine-rust system would be very useful to another part. For example, similar factors would be hypothesized and thus more easily found and studied. A breeding scheme based upon this principle may enable the tree breeder to establish more easily a balance in an unbalanced system or prevent an imbalance in a presently balanced system.

PROPOSED USE OF NATURAL MODELS

We propose that a new resistant population of western white pine be patterned after the combinations of factors that are presently protecting the highly resistant white pines (*P. armandii*, *P. wallichiana*, *P. koraiensis*, and *P. cembra*) from severe blister rust damage. This scheme would take advantage of the fact that the factors for resistance in the highly resistant white pines have already stood the test of time and are present in pines very closely related to western white pine. Some or all of these factors may be useful. However, there may be other factors in western white pine that may be more useful. Eventually all factors should be tested for stability. But the beauty of using "balanced symbiosis" as a model is that it allows the tree breeder to follow a priority list. He can select first those factors that are stable under "balanced symbiosis," and in the meantime be testing the stability of new factors.

It is important to point out that selection of a factor for resistance, by using the model system, would be based on its ability to protect western white pine from blister rust while remaining stable and not on the number or kinds of genes involved.

Of course, there is a great deal of information needed before we can begin to utilize the model. This would be equally true for other breeding methods. But in using "balanced symbiosis" we are following a natural plan that requires less speculation than the use of more artificial plans. Also, studies of "balanced symbiosis" could yield information of great value in understanding the evolution of host-parasite systems.

THE "KNOWLEDGE GAP"

In 1962 it was estimated that 10,000 questions had to be answered before a man could be landed on the moon and returned to earth. This venture, of course, was successful. However, many scientists involved with space exploration did not feel that they were ready to place a man on the moon. They thought the risk factor was still too high. In other words, not all the questions were answered.

A similar philosophy would be useful for producing a new population of blister rust-resistant western white pine. One would prepare a list of questions. Then at certain intervals he would tally the questions answered while adding new questions that may have arisen. Consequently, once enough information is accumulated to estimate the risk of failure the decision can be made to go ahead with the production of this new population.

The following list of general questions reflects our lack of knowledge. Each breeding program should establish a detailed list of questions for its specific host-parasite system.

1. Do the Eurasian pines-*Cronartium ribicola* systems represent a "balanced symbiotic" condition?

2. Does the "balanced symbiotic" condition for both the hard and soft pines reflect a common evolutionary history resulting in a common set of factors for resistance?

3. Where is the gene center of white pine blister rust?

4. What are the sites, mechanisms, and inheritance of the factors for resistance in each pine host-stem rust system?

5. What is the variation in aggressiveness, virulence, and other characters of the rust organism in each pine host-stem rust system?

6. What are the frequencies of each identifiable gene in each complete pine host-stem rust system?

7. What are the effects of epidemiological factors on the establishment and maintenance of "balanced symbiosis"?

8. Is there a genetic relationship between resistance genes and genes controlling other fitness and quality characters?

9. What are the mechanisms of genetic variation in the stem rusts?

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FLOOR DISCUSSION

VAN ARSDEL: If you are determining races on the leaf spot stage of your infection, how do you separate something like "*Coleopsorium jonesii*" from the rust if you have spores of that in your nursery, or do you carry them through to maturity--to aeciospores?

MCDONALD: Of course, we were initially very concerned about the specific identity of these individual spots. We looked at 20,000 spots in our nursery beds, and made histological collections of 100 of these spots representing seven different lesion classes that we had defined at that time. This past winter we carried out a microscopic analysis of these sections and found the typical pseudosclerotium in four lesion types that you saw yesterday. There were two types that did not have the pseudosclerotium; therefore, we threw these out. Also, they represented less than 1 percent of the 20,000 spots that we catalogued.

VAN ARSDEL: How would you separate *Cronartium* mycelium from *Coleosporium* mycelium?

MCDONALD: There was another factor involved. We were able to classify plants, individual seedlings, as having all red spots or all yellow spots, and so on. Many of the plants supporting only red spots and only yellow spots produced aeciospores this past spring.

BEGA: Where did you get these different races? Were they from geographically different areas?

MCDONALD: The inoculum used in the 1964 progeny tests, on which the race hypothesis is based, were obtained from a mile-long section of Hobo Creek here in Northern Idaho. The principal *Ribes* species involved was *hudsonianum* var. *petiolare*. We collected from individual bushes and mixed the leaves. Hopefully we had a fairly uniform distribution of inoculum over the test. But, let me point out that while this race hypothesis was made on the 1964 test it has subsequently been tested on the 1966 test. This test was inoculated 2 years later with inoculum obtained from the same area. We realize that we haven't really proven the existence of pathogenic races, but we have hypothesized the system and tested it using 10,000 seedlings, 1,000 seedlings per family in ten families.

HOFF: I would like to add a little here. The percentage of yellow spots was 60 whereas the percentage of red spots was 40 in the 1964 progeny. We got the same proportion in the 1966 progeny tests.

MCDONALD: That brings to mind another observation. When we classify the individual seedlings, we observe seedlings with no spots, seedlings with only red spots, seedlings with both red and yellow spots, and seedlings with only yellow spots. We looked at the frequency of needle lesions on the seedlings with only red spots and it averaged four lesions per 25 inches of needles. The frequency of lesions on trees with only yellow spots averaged six lesions per 25 inches, and seedlings with both types of spots averaged 10 lesions per 25 inches.

KINLOCH: Dr. Hoff, you mentioned that the endemic rusts are apparently living in a state of balanced symbiosis in which biological damage was not too severe--just economic damage. I take exception to this. I think the biological damage is very severe, and I think you only have to look at Harry Powers' slide this morning to be convinced. The mortality and selection pressure against the host species is quite severe in many of these rusts, especially in juvenile stages of the host, and therefore balanced symbiosis may not come from this uniform resistance that you were talking about, but rather from other specific resistance factors carried in the population at intermediate frequencies. At least this is an equally plausible hypothesis, I think. Secondly, I'd like to make another comment on your proposition that species in the same genus may carry the same resistance factors. I think it's worthy of note that red pine, as Harry Powers points out, is apparently resistant to all rusts, both endemic and exotic. Yet, presumably, the selection pressure has been on it for millenia. You can make a similar case for short-leaf pine resistance against fusiform rust in the South. These species, although closely related to other endemic species, have maintained a very high and stable resistance. I think this should make one pause before *a priori* assuming specific resistance will inevitably become labile and break down.

HOFF: First, selection in a balanced symbiotic system would select for resistance factors that could be classified as either specific or uniform. We didn't want to imply that natural systems are controlled only by uniform resistance factors. But what we did want to do is to increase its importance in our thinking. Second, balanced symbiosis is based on the assumption that the balanced host parasite system is an interaction in and also with a particular environment. Man has spread *C. fusiforme* and *C. quercuum* and their hosts around and so now these diseases and especially *C. fusiforme* are no longer in balance. They are beginning to behave just like "exotic" diseases.

PATHOLOGY AND GENETICS OF TREE RUST RESISTANCE: MODERATOR'S SUMMARY

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We have just terminated the Friday morning panel, covering the pathology and genetics of tree rust resistance. During the past few hours several authorities presented excellent summarizing reports about different sections of our basic knowledge in this field.

Now, during the last 10 minutes I am expected to give some kind of a final summarizing outlook. This is a hard and almost impracticable task, for nobody wants to have a summary of several summaries. Consequently I would prefer to go a different way.

Having completed an inventory of the known information, we know just where we stand. Moreover we can state that much progress has occurred, especially during the last 5 years. But in spite of all that, we have good reason to face the unsolved problems of our field, for many of the most important and difficult questions remain unanswered. Let me tell you more concretely what I mean:

1. Infection biology, including mechanisms of resistance.--In several rust diseases of forest trees like *Cronartium ribicola*,[1] *Melampsora pinitorqua*, or *Peridermium pini*, up to now the process of infection is at least only partly known. As long as pathologists do not know how the fungus finds its way into the host and how it grows within the host tissues, it is difficult to understand much about resistance mechanisms. And if we ignore the existence of different mechanisms of resistance, we sooner or later are led to something like an "everything or nothing" standpoint. Perhaps we already have taken some steps in this direction, for those forms of resistance like tolerance or recovery ability, which in my opinion may be of special importance for rusts on forest trees, were seldom mentioned here. So I would like to stress that increased activities and more investigations concerning the basic questions of infection and resistance biology are very much needed.

2. Problems of pathogen identification and differentiation.--We now have good evidence that racial differentiation exists within the rust fungi *Cronartium quercuum*, *Cronartium ribicola* and *Peridermium pini*. There is no doubt that these findings increase the tree-breeders' risk. So, further investigations about the size of race spectra and their geographical distribution are evident. Although it appears different the situation in poplar rusts in general is similar to that in pine rusts. In both cases pathologists have difficulties in identifying the pathogen, here the species, there the race. Again, however, in order to control the rust we first must know practically every detail about its biology and pathogenicity. Otherwise drawbacks cannot be avoided. Consequently

[1] *Authorities for Latin binomials are given in the subject index.*

there is little doubt where the investigations have to go. As soon as suitable test material is available, we need an adequate test system for rust races and rust species.

ENVIRONMENT AND ATTACK

The mere interactions between meteorological factors and infection biology perhaps can give some practical hints on how to control a disease with simple methods. With the exception of white pine blister rust on *Pinus strobus* we know very little if anything at all about this side of the host-pathogen-environment complex in forest tree rusts. This should be reason enough why interactions between infection intensity and climatic conditions and especially connections between degree of resistance and nutrition of the host should be investigated more intensely now.

Finally I would like to point out that experts who have observed the development of our field during recent years agree that interest in the fundamental biological investigations and experiments has markedly increased. The future appears bright, the more since these findings could also help those people who work on other control aspects of the same problem, for we should not forget that resistance breeding is only one method for protecting forest trees against rust fungi.

PANEL V

BREEDING SCHEMES FOR MASS-PRODUCTION OF RUST RESISTANT TREES

Norman E. Borlaug, MODERATOR

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BREEDING OF WHITE PINE FOR RESISTANCE TO BLISTER RUST AT THE INTERSPECIES LEVEL

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ABSTRACT

The results of interspecific hybridization of white pines at Maple, Ontario, Canada, from 1956 to 1965 are presented. Five species, *Pinus griffithii* (syn. *P. wallichiana*), *P. monticola*, *P. parviflora*, *P. peuce* and *P. strobus*, can be easily crossed with each other but with reduced seed set and somewhat reduced fertility in the F_1's and F_2's, and backcrosses, including some triple and multiple crosses, are reported also. Some precocious flowering was observed in hybrid populations resulting from crosses of *P. peuce* with all other members of this closely related group. The use of this precocious flowering as a means of reducing the time periods during gene transfer from one species to another is discussed.

A white pine breeding project was initiated at the Southern Research Station of the Ontario Department of Lands and Forests at Maple, Ontario, Canada, in 1946. The aim of this project was to develop new strains of native white pine (*Pinus strobus* L.) having resistance to blister rust, caused by *Cronartium ribicola* J. C. Fisch. ex Rabenh., and other desirable traits for growing in southern Ontario. Promising white pine materials were assembled for breeding work at both the intraspecific and interspecific levels. The results with interspecific hybridization will be discussed in this paper.

Several exotic species, closely related to native white pine, namely *P. peuce* Griseb., *P. griffithii* McClell. (syn. *P. wallichiana* A. B. Jacks.) and *P. parviflora* Sieb. & Zucc. (includes *P. himekomatsu* Miyabe & Kudo and *P. pentaphylla* Mayr) are more resistant to blister rust than *P. strobus* (Spaulding, 1925; Tubeuf, 1926, 1933). In addition, breeding materials of several other white pine species were of interest because of their largely unexplored breeding potentials.

The work started from scratch on former farm land. It took about 10 years to establish a nursery and other propagating facilities, to assemble a collection of breeding materials in the form of seedlings and grafts, and to work out a reasonably satisfactory method of growing black currants (*Ribes nigrum* L.) under the climatic conditions of this Station. The first interspecific crosses were made on native older white pine at the Station and in the vicinity; later, as grafts of the new acquisitions began to flower more abundantly, most of the hybridization work was shifted to these.

The first crosses were largely failures, as the few seedlings obtained perished in the seed beds and succumbed to blister rust. Starting from 1956, reasonably satisfactory results began to accumulate. Tables 1 to 3 list all the crosses made between 1956 and 1965, with the results obtained. These comprise 20 combinations between species of the subsection *Strobi* of Critchfield and Little (1966), seven of the subsection *Cembrae* and 12 between *Strobi* and *Cembrae*. There are 21 new crosses, 3 successful with *Strobi*, one with *Cembrae* and two between *Strobi* and *Cembrae*. In addition, there are three F_2's and 14 backcrosses, all of *Strobi*, as well as 14 triple and multiple crosses, ten of *Strobi* and four between *Strobi* and *Cembrae*, the latter unsuccessful.

Crosses of particular interest to the white pine breeding project are those between *P. strobus* and *P. griffithii*, *P. monticola* Dougl. *P. parviflora* and *P. peuce*. Triple and multiple crosses between these species were also largely successful. The other crosses were mostly exploratory, to gain more insight into the crossability patterns within and between *Strobi* and *Cembrae*. In general, the results confirm the information assembled by Wright (1959) and Little and Righter (1965).

The crosses *P. armandii* Franch. x *P. lambertiana* Dougl. and *P. koraiensis* Sieb. & Zucc. x *P. lambertiana*, involving a pine species of great economic importance, were successful without resorting to embryo culture which was necessary in the respective reciprocal crosses (Stone and Duffield, 1950). In nearly all interspecific crosses the number of full seeds per cone and percentage of full seeds obtained were lower than in the intraspecific crosses *P. strobus* x *P. strobus*. This applies also to the F_2's and backcrosses and to the triple and multiple crosses. Thus, breeding of white pines at the interspecific level must take reduced seed yield into account, at least in producing the F_1 and F_2 generation hybrids.

The information obtained thus far indicates the presence of a relatively closely related group of five white pine species: *P. griffithii*, *P. monticola*, *P. parviflora*, *P. peuce* and *P. strobus*, at least three of which (*P. griffithii*, *P. monticola*, *P. strobus*) are of major economic importance. They are easily crossable with each other, with some loss in seed production following interspecific hybridization, and in fertility of the resulting F_1's.

Previously, it was found (Heimburger, 1961) that *P. peuce* carried a dominant gene or genes for precocious flowering which was clearly expressed at the interspecific level. This has been confirmed in the present crosses. All crosses of *P. peuce* with species of the closely related group mentioned above have yielded some seedlings with precocious flowering.

Three of the five species of the group are known to be more resistant to blister rust than *P. strobus* and *P. monticola*. This resistance is inherited in at least some hybrids with the more susceptible species and is presumed also to depend on the breeding materials used. Compared with *P. strobus*, no exotic species have proved to be as suitable for forestry purposes in climatic and ecological adaptation and resistance to certain native pests. This probably also applies to the other four species in their respective homelands.

Because of these findings and because of the decreased fertility of the interspecific F_1's, the most promising approach in long-range resistance breeding is the introduction of additional resistance genes from

Table 1. Single interspecific crosses of selected taxa within the subgenus *Strobus* section *Strobus* of the genus *Pinus*

Species	Flowers pollinated	Cone set percent	Empty seeds per cone	Full seeds per cone
P. strobus x *P. strobus*	4856	16.4	8.9	18.8
[a]*P. monticola* x *P. pentaphylla*	40	22.5	16.5	5.3
[a]*P. peuce* x *P. pentaphylla*	193	26.1	6.2	7.2
P. griffithii x *P. pentaphylla*	140	12.9	14.8	2.8
[a]*P. parviflora* x *P. griffithii*	19	36.8	2.0	1.6
P. strobus x *P. parviflora*	1373	35.5	8.9	6.0
[a]*P. flexilis* x *P. pentaphylla*	19	0	--	--
[a]*P. cembra* x *P. pentaphylla*	10	70	--	--
P. parviflora x *P. cembra*	126	0	--	--
[a]*P. parviflora* x *P. albicaulis*	330	26.7	--	--
[a]*P. pentaphylla* x *P. lambertiana*	106	39.6	--	--
P. monticola x *P. monticola*	201	1.0	15.0	1.5
P. monticola x *P. peuce*	668	10.3	34.4	3.1
P. monticola x *P. griffithii*	54	0	--	--
[a]*P. griffithii* x *P. monticola*	24	37.5	--	--
P. monticola x *P. strobus*	438	13.7	9.8	10.1
P. strobus x *P. monticola*	226	.4	--	--
[a]*P. monticola* x *P. cembra*	62	0	--	--
P. peuce x *P. strobus*	2862	28.7	15.4	5.5
P. strobus x *P. peuce*	3221	17.4	12.2	10.2
[a]*P. peuce* x *P. griffithii*	?	?	20.5	1.2
[a]*P. peuce* x *P. flexilis*	23	60.9	--	--
P. griffithii x *P. strobus*	756	33.7	16.3	4.7
P. strobus x *P. griffithii*	95+	(8.4)	14.7	3.0
[a]*P. cembra* x *P. griffithii*	45	60	--	--
[a]*P. armandii* x *P. albicaulis*	74	54.1	24.3	0
[a]*P. armandii* x *P. lambertiana*	79+	54.4	100	.6
[a]*P. cembra* x *P. albicaulis*	104	24.0	19.8	2.4
[a]*P. cembra* x *P. armandii*	33[b]	15.1	7.8	.2
[a]*P. cembra* x *P. flexilis*	32	0	--	--
[a]*P. cembra* x *P. koraiensis*	49	81.6	11.1	1.1
P. cembra x *P. lambertiana*	16	18.7	--	--
P. flexilis x *P. cembra*	31	0	--	--
P. flexilis x *P. koraiensis*	10	0	--	--
[a]*P. koraiensis* x *P. albicaulis*	324[b]	10.5	2.9	.2
[a]*P. koraiensis* x *P. armandii*	34	0	--	--
[a]*P. koraiensis* x *P. cembra*	31	0	--	--
[a]*P. koraiensis* x *P. flexilis*	44	20.4	--	--
P. koraiensis x *P. lambertiana*	644	9.8	1.5	2.3

[a] new cross
[b] hybridity doubtful

Table 2. F_2 and backcrosses of selected taxa within the subgenus *Strobus* section *Strobus* of the genus *Pinus*

Species	Flowers pollinated	Cone set percent	Empty seeds per cone	Full seeds per cone
(*P. monticola* x *P. parviflora*) x *P. pentaphylla*	91	83.5	12.6	4.7
P. griffithii x (*P. griffithii* x *P. parviflora*)	173	35.3	16.5	4.6
(*P. griffithii* x *P. parviflora*) x *P. griffithii*	92	0	--	--
(*P. parviflora* x *P. strobus*) F_2	186	62.4	1.5	.1
P. parviflora x (*P. parviflora* x *P. strobus*)	180	82.2	26.0	1.5
(*P. parviflora* x *P. strobus*) x *P. parviflora*	2	0	--	--
(*P. parviflora* x *P. strobus*) x *P. strobus*	39	51.3	5.7	.1
P. strobus x (*P. strobus* x *P. monticola*)	136	30.1	5.3	26.0
(*P. peuce* x *P. strobus*) F_2	1206	43.5	7.9	3.4
P. peuce x (*P. peuce* x *P. strobus*)	40+	?	24.2	10.1
P. strobus x (*P. peuce* x *P. strobus*)	405	25.4	8.5	6.5
(*P. peuce* x *P. strobus*) x *P. strobus*	42	14.3	8.3	7.7
(*P. griffithii* x *P. strobus*) F_2	770	47.4	15.4	7.2
(*P. griffithii* x *P. strobus*) x *P. griffithii*	136	12.6	4.5	1.0
P. griffithii x (*P. griffithii* x *P. strobus*)	682	42.1	31.1	8.1
(*P. griffithii* x *P. strobus*) x *P. strobus*	419	18.1	8.9	5.0
P. griffithii x (*P. flexilis* x *P. griffithii*)	50	24.0	23.2	4.3

Table 3. Triple and multiple interspecific crosses of selected taxa within the subgenus *Strobus* section *Strobus* of the genus *Pinus*

Species	Flowers pollinated	Cone set percent	Empty seeds per cone	Full seeds per cone
(*P. griffithii* x *P. strobus*) x (*P. griffithii* x *P. parviflora*)	54	3.7	5.0	1.5
(*P. griffithii* x *P. strobus*) x *P. pentaphylla*	146	29.5	4.9	.7
P. parviflora x (*P. flexilis* x *P. griffithii*)	4	100	4.5	2.5
(*P. parviflora* x *P. strobus*) x (*P. flexilis* x *P. griffithii*)	32	75	8.2	.04
P. pumila x (*P. parviflora* x *P. strobus*)	4	0	--	--
(*P. monticola* x *P. griffithii*) x (*P. griffithii* x *P. strobus*)	48	43.7	37.0	19.2
(*P. strobus* x *P. peuce*) x *P. griffithii*	?	?	6.7	.8
P. griffithii x (*P. peuce* x *P. strobus*)	60	0	--	--
P. peuce x (*P. flexilis* x *P. griffithii*)	68	45.6	17.8	1.4
(*P. strobus* x *P. peuce*) x (*P. flexilis* x *P. griffithii*)	13	64.6	14.1	.9
P. strobus x (*P. flexilis* x *P. griffithii*)	68	22.1	25.9	4.1
(*P. griffithii* x *P. strobus*) x *P. albicaulis* (not hybrids)	26	42.3	7.1	2.3
(*P. griffithii* x *P. strobus*) x *P. lambertiana*	25	8	0	--
(*P. griffithii* x *P. strobus*) x *P. cembra*	25	4	0	--

the exotic species (donor species) to the native species (receptor species) by means of backcrossing with the native species as the recurrent parent. This will lead to the production of synthetic varieties. A successful incorporation of exotic resistance genes into the genome of a native species should result in strains with fully recovered fertility and adaptation, permitting free gene exchange with the most advanced strains of the native species at any point of an intra-species resistance breeding program.

The time factor is the most important bottleneck in such a breeding program, consisting of artificial, guided introgression from one or several exotic species into the native species. It takes about 25 years for seedlings of *P. strobus* to begin flowering on a sufficient scale for breeding purposes. It will probably take at least two backcrosses, each requiring 25 years, to successfully incorporate exotic resistance genes and thus to broaden the gene pool of the native species. This means a period of about 75 years, and any means to shorten the breeding cycle of such materials will be of major importance.

To date there are two known methods of shortening the breeding cycle of forest trees. One is the application of growth retardants and flower-promoting hormones, and the other is artificial aging by shortening the juvenile phase in a growth chamber (Dormling, Gustafsson, and von Wettstein, 1968). A third method, herewith proposed, is the introduction of dominant genes promoting flowering, in this case genes from the precocious *P. peuce* mentioned above. It should be possible to incorporate precocious flowering from *P. peuce* into all the other related white pine species of economic importance by means of appropriate backcrosses. Since precocious *P. peuce* and some of its hybrids begin to produce female flowers at age 5 and are flowering abundantly at age 7, this incorporation should require at most 20 years. It is quite possible that flowering of precocious materials can be further hastened by appropriate manipulation of the environment.

These precocious types are not suitable for direct use in forestry because abundant flowering is usually achieved at the cost of wood production and longevity, resulting in small, short-lived trees. However, the precocious types could be used as immediate receptors of new resistance genes to be introduced from any of the other related species. Such a precocious receptor type could then be used to absorb the low fertility and poor adaptation following interspecific hybridization with promising new breeding materials from any exotic donor species. In three generations, i.e., in about 21 years, this program should produce strains carrying the new genes in a form freely exchangeable with the most advanced materials obtained at any point of the intraspecific breeding.

Research with precocious *P. peuce* should be initiated to ascertain how many dominant genes for precocious flowering there are available and in what manner they can best be used for the purposes intended. The end product should be a strain carrying the relevant dominant genes for precocious flowering in a heterozygous condition, so they can easily be eliminated in the final backcross to the receptor species.

In grafts of *P. strobus* there is usually a gap of about 15 years between female and male flowering (Wright, 1964). This has been a most serious handicap in our white pine breeding work. Only recently Chiba (1965) has found a method of inducing male flower formation in grafts of *P. strobus* of flowering age. The method consists of pinching off all

vegetative growth on young grafts in early spring. The resulting new growth from axillary buds then produced male flowers. We have had a similar experience recently with young grafts that grew too large for proper inoculation with blister rust. Perhaps this method can be applied to other white pine species, at least to those of the group with which we are dealing. This could be of help in more rapid breeding work, and also with the precocious receptor strains envisaged above. It should be possible gradually to develop such precocious receptor strains of all the economically important white pine species and thus to accelerate resistance breeding on an international scale.

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FLOOR DISCUSSION

KEDHARNATH: Dr. Heimburger, as one who has had really wide experience in species hybridization of pines, do you visualize the time when you can use hybrid seeds between two species when you have identified two very good clones, and if so, how do you propose to go about it?

HEIMBURGER: This of course has been proposed by John Wright. When he first published his results on white pine hybridization in Philadelphia, he thought he could mass produce hybrid seed for direct use in forestry. I don't believe very much in that, because there may be some hidden pests. There may be a fungus or insect that doesn't attack the native

species at all which may attack the F_1 very badly and then you're sunk. I'd rather say that the F_1 is a means to an end. That we have to have the F_2 or a backcross before we can do anything with it, and we have as yet not discovered a method of producing F_2's without first producing F_1's.

BINGHAM: What is the frequency of the precocity in *P. peuce*?

HEIMBURGER: About 1/3.

BORLAUG: Is this pretty much the same frequency in the interspecific crosses?

HEIMBURGER: Yes. So the gene must be quite widespread in *P. peuce*.

CAMPANA: How long have you been able to store pollen of white pine and retain viability and under what conditions?

HEIMBURGER: We store white pine pollen over silica gel in a dessicator at 20 below zero F., and we can store it for 2 years, but we don't like to store it more than 1 year.

GERHOLD: Dr. Heimburger, can you make any general observations about adaptation and growth form of the various types of hybrids, including F_2's, backcrosses, and triple hybrids?

HEIMBURGER: Well, I think that the cross *P. peuce* x *P. griffithii* is much more promising than the cross *P. peuce* x *P. strobus*, because the F_1's with *P. strobus* are rather miserable trees and they grow slowly, and are infected by several insects, which *P. peuce* and *P. strobus* are not. The *P. peuce* x *P. griffithii* approach is probably better in the long run; *Pinus peuce* of course, grows farthest north in our area of all the exotic species. We have the native white pine growing up to Lake Nipigon and then *P. peuce*, *Pinus monticola* and *P. griffithii* are more tender. So we have used *P. peuce* quite a bit more than any other because of that. We have grown it up north and tested it and I would say that hybrids between *P. peuce* and *P. griffithii* are quite promising with us. We have several *P. griffithii* hybrids in parks in Toronto where people have obtained seeds from Italy under the name of *P. griffithii*, and of course the hybrids grow faster, and survive under hard conditions and they are now placed in parks under a *P. griffithii* label. They are not *P. griffithii*; they are hybrids. The backcrosses to *P. strobus* are quite good. They can easily be crossed with *P. strobus*. *Pinus peuce* is not so easy, and of course, *P. parviflora* is the most difficult.

ZUFA: In F_2 and following crosses, as well as in the backcrosses, we have segregation back to the original species and forms and we sometimes produce very heterogeneous populations. I wonder what your opinion is about that and how do you intend to use such populations in forestry practice?

HEIMBURGER: I don't think that we should worry much about uniformity because the first backcross of course will be under laboratory conditions, so to speak. The second backcross is of interest to forestry, and by that time the variations should be reduced to practical levels. In fact, it would be very useful to have some variation to maintain expression of dominance and we propose to screen them for blister rust resistance every time and then let them grow under plantation conditions, and eliminate all the poor ones.

BORLAUG: I would agree with you, Dr. Heimburger, that in the first backcross there is plenty of variation and so you can pick the trees you want.

DE JAMBLINNE: Have you noticed any differences between hybrids when *P. peuce* pollen of different provenances are used?

HEIMBURGER: Well, not exactly. We have, of course, as I showed on Wednesday, several populations of *P. peuce* from different areas, and the one from Finland seems to be better than the others. *Pinus peuce* is very uniform, but in resistance, of course, all of the problems here are now in weevil studies. *Pinus peuce* is extremely variable with differences between populations and from tree to tree to weevil damage. But there is not too much variation in hybrids.

VAN ARSDEL: How many seed sources of *P. peuce* have you been using?

HEIMBURGER: Seed sources, as I showed you before, number about a half dozen or so, but we have collected scions from many arboreta in Europe and North America of the flowering phase and have then pollinated them with white pine.

VAN ARSDEL: Those are from different arboretums; they are not from different parts of the range in the Balkans.

HEIMBURGER: No, we don't know where they come from. And the same thing with *P. griffithii*. We have obtained material from several places and largely of unknown origin but still many of them are quite good. In fact, one tree I showed you in the slides accompanying my Wednesday paper is quite promising.

THE LONG-RANGE OUTLOOK FOR PRODUCTION OF RUST RESISTANT TREES BY INDUCED MUTAGENESIS

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ABSTRACT

In crop plants induced mutagenesis has been effectively used and an array of mutants has been assembled. In the past, more attention was directed to selecting macromutations. More recently the importance of micromutations or polygene mutations has been recognized for improvement of quantitative characters. Chemical mutagens seem to hold promise for increasing the mutation frequency as compared to physical mutagens. Right choice of the mutagen and improvement in the methods of screening the mutants can increase the value of induced mutagenesis as a tool in breeding for disease resistance.

INTRODUCTION

In the last 18 years or so a large number of induced morphological and physiological mutants has been assembled for a number of crop plants. Several reviews have appeared that cover this subject of induced mutation. Some of these are: Konzak (1956), MacKey (1956), Singleton *et al.* (1956), Smith (1958), Stübbe (1958), Prakken (1959) and Gaul (1958, 1964). Intraspecific macromutations (mutations with major gene effects) are the most common type of mutations selected. Small mutations or micromutations (mutations with minor gene effects) have not received the attention they deserve from plant breeders. In recent years the importance of these small mutations in breeding programs has been emphasized by Nybom (1954), Gregory (1955a,b, 1956) and Gaul (1958).

Most plant attributes of interest to breeders are quantitative characters which are controlled by many genes or polygenes. It is reasonable therefore to expect that mutation of the polygenes will affect a quantitative character in a measurable way. In fact, there is some evidence of this in the studies of Gregory (1955a,b, 1956) on peanuts with regard to genetic variance for yield in the progenies of normal appearing M_2 plants which were selected at random. He succeeded in selecting mutants with higher yielding capacity. Oka, Hayashi, and Shiojiri (1958) in rice and Moës (1958, 1959) in barley have also reported small mutations exerting a quantitative effect in respect to a number of characters.

In the field of induced mutation for disease resistance, the first report of positive results is that of Freisleben and Lein (1942) in barley for resistance to mildew. Since that time many workers have

reported on obtaining useful resistant mutants. Resistance to Victoria blight, stem rust, and crown rust has been reported in oats; to stem rust and stripe rust in wheat; to mildew in barley; to rust in flax; to leaf spot and stem rot in peanuts, and to anthracnose in bean (Konzak, 1954; Frey, 1954; Shebeski and Lawrence, 1954; Frey and Browning, 1955; Flor, 1955; Konzak *et al.*, 1956; Myers *et al.*, 1956; Down and Anderson, 1956; Hansel and Zakovsky, 1956; Gregory, 1956; Konzak, 1959; Cooper and Gregory, 1960; Favret, 1960a,b; Bhatia, Swaminathan, and Gupta, 1961). These examples illustrate that it is possible to obtain disease-resistant mutants through induced mutagenesis.

It may be argued that the frequency of these mutations is still too low for effective use. It should be possible, as Konzak (1956) and Gaul (1964) have predicted, that improved efficiency in the use of mutagens and screening procedures may increase not only frequency of mutations but also their identification and recovery. Various chemical mutagens may substantially increase the mutation frequency. For example, ethyl-methane-sulphonate, diethyl-sulphate and ethylene imine are potent mutagens in higher plants (Heslot, *et al.*, 1959; Ehrenberg, Gustafsson, and Lundquist, 1961; Swaminathan, Chopra and Bhaskaran, 1962; Konzak *et al.*, 1965). Then too, screening procedure for disease-resistant genes are most efficient when plants can be screened at the seedling stage under artificially created epiphytotics. The technique developed by Wheeler and Luke (1955) also merits attention. Using the toxin produced by the pathogen, *Helminthosporium victoriae* Meehan & Murphy, as a screening agent, they tested two varieties of oats for resistant variants. In 100 bushels of oats screened (approximately 45 million grains), 973 blight-resistant seedlings were obtained.

RADIATION EXPERIMENTS WITH FOREST TREE SPECIES

Radiations from physical sources, i.e., X-rays, gamma-rays and neutrons, have been widely used with forest tree material with two objectives in view. One objective was to study the immediate effects of acute irradiation or radio-sensitivity and cumulative effects of chronic irradiation on the developmental process of the treated material (Gustafsson and Simak, 1958; Simak, Ohba, and Suszka, 1961; Snyder, Grigsby, and Hidalgo, 1961; Mergen and Stairs, 1962; Okunewick, Herrick, and Carlsen, 1964; Yim, 1964; Privalov, 1964, 1965; LaCroix, 1964; Stairs, 1964; Sparrow *et al.*, 1965; Bevilacqua, 1965; Mergen and Cummings, 1965; McMahan and Gerhold, 1965; Osborne and Lunden, 1965; Murai and Ohba, 1966; Kedharnath, 1966, 1967, 1968, 1969; Rudolph, 1967; Miksche and Rudolph, 1968). The second objective was to induce genetic changes or to overcome incompatibility barriers (Rudolph, 1965, 1966). Pollen irradiation appears to be of particular usefulness in tree species (Stairs and Mergen, 1964). The major advantages of this approach, compared with using seed, seedling or other plant parts for irradiation, would be (1) a reduction in time from irradiation to scoring the progeny and (2) absence of possible diplontic selection against affected cells.

EXPERIMENTS WITH CHEMICAL MUTAGENS ON FOREST TREE SPECIES

Hanover (1964) treated seeds of *Pinus monticola* Dougl. with ethyl-methane-sulfonate (EMS). The objects were to determine the physiological effects of the mutagen on the seeds and seedlings and to attempt to induce genetic resistance against the blister rust fungus (*Cronartium ribicola* J. C. Fisch. ex Rabenh.). Kedharnath (1968) treated seeds of *P. roxburghii* Sarg. with EMS and found that germination, hypocotyl length and survival were affected with increasing concentration. Yim (1963) using seeds of *P. rigida* Mill. for treatment with EMS also found a decrease in germination and seedling growth with increasing concentration of EMS. Similar studies by Kedharnath (1969) on *Dalbergia sissoo* Roxb., a broad-leaved species, comparing results obtained with those reported earlier for *P. roxburghii*, showed that (1) at pH 9 the sensitivity of both species to the mutagen was higher than at pH 5 and (2) *D. sissoo* was more sensitive than *P. roxburghii*.

Hanover and Hoff (1966) treated *P. monticola* pollen with EMS. They obtained good seed set by using treated pollen in controlled crosses, but the seedlings are yet to be scored. Kedharnath (*unpublished*) treated pollen of *Morus alba* L. with EMS and used it in controlled crosses with good seed set. Here again seedlings are yet to be scored.

POSSIBLE APPROACHES TO MUTATION-INDUCED RESISTANCE

The basidiospores of *C. ribicola* are formed on *Ribes* spp. Infection of white pines with these spores occurs during cool moisture periods. Since the basidiospores are the product of meiosis following nuclear fusion in the telutospores, each basidiospore is potentially unique. This uniqueness could also be true for the character of pathogenicity on the pines and will naturally depend upon the number of genes conditioning pathogenicity of the fungus in relation to the pine host.

If pathogenicity is controlled by one or a few genes, the possible number of unique types of pathogenicity would also be few. In such a case, major gene-conditioned resistance in the host may be useful. On the other hand, if a large number of genes control pathogenicity of the fungus, the host plants will be exposed to a large number of unique types of spores. In such a situation, it would be more profitable and even essential to look for and exploit polygene-controlled field or horizontal resistance. Unfortunately we have little information on this aspect.

Flor (1955) working with linseed rust, has shown convincingly that there exists a 1 to 1 relationship between the genes for pathogenicity in the fungus and genes for resistance in the host. If we assume that a similar relationship also holds in the present case then a consideration of the available information on the nature of resistance in the host plant, i.e., pines, would be of interest.

We still do not have definite information about the number of genes conditioning resistance to blister rust in the different species of native and exotic white pines that have been studied in the United States and Canada. There may be more than one source of resistance within the same species and some of these sources may be conditioned by a single gene, some by two or more and some by polygenes. That such a situation can exist is supported by evidence for several other vegetable and crop plant diseases including rust of wheat. According to Heimburger (1962)

blister rust resistance in *P. strobus* L., *P. monticola*, *P. peuce* Griseb, *P. parviflora* Sieb. & Zucc. and *P. wallichiana* A.B. Jacks. (syn. *P. griffithii* McClell.) is largely polygenic since resistance of the interspecies crosses was often expressed in an additive manner. He also reported on a possible major gene controlling rust resistance in *P. wallichiana* which is expressed as a sloughing off of infected needles. Bingham, Squillace, and Patton (1956) found that rust resistance of some of the resistant selections of *P. monticola* can be transmitted to the progenies. Bingham, Squillace, and Wright (1960) estimated the broad-sense and narrow-sense heritability of rust resistance in *P. monticola* as 86 and 68 percent respectively. Bingham (1964, 1966) speculated that blister rust resistance in *P. monticola* and *P. strobus* is controlled by polygenes.

As has been pointed out in the earlier sections of this symposium, it would seem necessary to look for field resistance in the pine species. The aim of mutagenic treatment in this context would be to increase the variability and by subsequent conventional breeding procedures accumulate more and more minor genes for resistance. In this connection the procedures suggested by Borlaug (1966), regarding different forms of recurrent selection developed by corn workers, could be used with appropriate modifications.

Indeed it may be worthwhile to begin with the selected resistant trees as the basic material. Pollen collected from these trees can be irradiated and used in controlled pollinations of other resistant trees. The resulting progenies could be screened for resistance and the desirable seedlings cloned. These clones can then be used for laying out seed orchards. From these seed orchards we can hope to get further concentration of genes for resistance from which a second wave of more resistant seedlings can be raised. Repeated irradiation in every generation can help in increasing the variability and thus raise the ceiling of resistance that can be obtained.

Interspecific hybrids between the desirable species like *P. monticola* and *P. strobus* or between one of these species and other donor species such as *P. wallichiana* are currently being exploited for increasing resistance to blister rust. Little is known as yet about the nature of chromosome pairing in the F_1 hybrids. If there is any lack of homology, even if only at the cryptic level, subjecting F_1 hybrids at the appropriate stage to irradiation may increase the frequency of recombination and thus facilitate the task of transferring genes for resistance from the donor genome to the recipient genome.

Recent work by Briggs, Flor, Favret, and others has shown that there are numerous genes that often are not distributed at random over the genome of the host plant but tend to be grouped in genetical segments concentrated in a few chromosomes (Gustafsson and Mergen, 1964). If this is the situation in pines, high blister rust resistance may be achieved very quickly if the right block of genes is transferred through interspecies hybridization. Thus, procedures that increase the frequency of recombination may substantially aid the breeder.

In conclusion it may be said that artificial mutagenesis cannot replace hybridization and recombination. It is an additional tool. However, its significance will increase to the extent we learn to predict the chromosome and gene changes which are produced by various mutagens (Gustafsson, 1960).

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FLOOR DISCUSSION

KINLOCH: There seems to be one problem with induced mutations; that of distinguishing between true mutations and an abnormal physiological response to radiation or whatever mutagen you are using. True mutation can't be proved until you are able to get flowering, seed, and subsequent segregation ratios in the offspring. Another approach that has been used very successfully in some plants, notably *Arabidopsis thaliana* Schur, is inducing by chemical mutagens, mutations in the apical meristem of a plant, and incorporating this mutation in subsequent divisions until it gets into the germ line of flowers. This gives a valid basis for really detecting whether you have a genetic mutation or just a physiologic response. Do you have any comment on that?

KEDHARNATH: I have no disagreement on what you have said, but I would like to approach it in a different way. When you use pollen for irradiation, you are dealing with a single cell in a sense, and you are widening plant selection and also cutting down the genetics and time from irradiation to scoring time. So, in pine breeding, pollen irradiation has a particular advantage compared to seed irradiation. True, in a cross-pollinated species there is no precise way of saying you have created the variation. The only thing we can do is to compare this initial population with the new population, and see whether we have increased the variability.

BLAIR: In your paper you state that most pines are open pollinated. In almost every instance, we have hardly begun to realize how much variation we have, let alone begin to tap it. I don't see how we could seriously consider using induced mutation in a situation like this until we have gotten much farther along in trying to tap what variability we do have.

KEDHARNATH: My suggestion is only that this is an additional approach. After selecting your plus trees, say you had 40 or 50 trees that you're working with there is a certain amount of variability available within those 50 trees. After general combining ability and all such experiments,

you find that you have eliminated some of the clones, and you bring down your base to 20 or 30 desirable trees. Inducing mutations will be an additional source of inducing minor alterations in this material and to that extent it can be useful, and also it may be useful in upsetting the fine balance that exists within the pathogen and the host.

BORLAUG: I'd like to make one comment about this kind of work. About 3 years ago Dr. George Varughese who did his work at the Indian Agriculture Research Institute produced, by mutation, a white seeded Sonora sixty-four, which was one of the introduced wheat varieties that fit very well in India. There is a series of alleles that influence grain color and Sonora sixty-four had one gene for red. White grain is preferred, it really constitutes a premium of about 20% on the market, and he came up with this gene. The plant itself was indistinguishable from Sonora sixty-four, in adaptation, yield and other characteristics, so that the trait couldn't be identified until the second generation after treatment. In the development of this kind of work, it's very important to grow a very large number of plants, and also you must have a very keen eye to examine these for very small differences. It's these small ones that you want. Not the big ones where there is a lot of injurious effects that go along with it.

PERSISTENCE OF RUST RESISTANCE

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ABSTRACT

Some pragmatic proposals are given on how to test host resistance together with precautions to take in releasing resistant stock to reduce the chance of experiencing rebounds in resistance breeding.

INTRODUCTION

The confrontation of *Pinus monticola*[2] with *Cronartium ribicola* has led to disaster wherever climatic conditions permitted the triangle of host, alternate host and parasite to function, i.e., wherever the pathogen could become aggressive to white pine. We should not believe that only the occurrence of modern man could bring about the disaster. Such processes are an integral part of evolution in living organisms. But modern man just does not like the idea of losing a valuable timber species. The decision to embark on breeding for resistance was not a "decision" in the conventional sense - there existed no alternative.

As was demonstrated in the research nursery, picking survivors in the field not only resulted in considerable genetic gain, if this term is applicable, but also provided the crucial service of bringing the survivors together. Trees cannot move and hence the severely hit parts of the host population could survive only by undergoing an intrinsic change of its genetic system. After test crosses were made, the progenies of a complete mating design were artificially inoculated. Typically enough, nobody talked about indirect selection for resistance by means of some biochemical or morphological trait, since for the sake of permanence a mere statistical relationship can never replace looking at the resistance traits themselves. This approach does not answer questions of selecting varieties for yield after infection becomes manifest in losses of trees and retarded increment of the survivors.

The resistance behavior of the progenies in crossing experiments proved beyond doubt that heritable variation for resistance exists in the host - how else could it be? -, and that the average percentage of healthy trees in the select progenies in the most critical stage of their life cycle ranged above the base population mean. This heritable

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[2] *Authorities for Latin binomials are given in the proceedings subject index.*

variation has to be the result of the differential frequency of certain rare preadapted genes, since the introduction of the pathogen meant a sudden and fundamental change of the host environment. This variation may or may not be related to provenance, depending on the adaptive significance of correlated gene effects.

The percentages of healthy trees are estimates of the probability that seedlings are not infected (or show no disease symptoms) under given conditions. But, strictly speaking, no information exists on whether these given conditions represent the environments where the select material will be planted in the future.

Should testing be put on a much broader base since differential response of host genotypes has to be envisaged as does variability in response to the spectrum of pathogen genotypes? I will not talk about horizontal vs. vertical resistance (van der Plank, 1968) at this point since I am unable to see the idea of this terminology. Evidence exists in forest trees (Schütt, 1964; Heybroek, 1969) that both general and specific resistance may occur in the varieties entering one and the same experiment. In fact, a certain individual may carry genes showing different types of variation.

THE PROBLEM OF PERSISTENCE

Many investigations have shown that resistance longevity depends on the type of genetic variation. Polygenically inherited resistance generally fails to provide immunity; consequently, the pathogen is allowed to complete its life cycle. But a certain level of the resistance attained lasts longer since a newly emerging pathogen genotype is less likely to overcome the host resistance. The risk in many instances has turned out to be greater if resistance was based only on a few major genes.

If the genetic basis of host resistance is broad enough, general resistance may prevail and one need not breed for resistance against specific fungal genotypes. To ascertain this condition, one has to utilize a large gene pool. It is also understood that one need not bother about loss of part of a resistant stock that we mass-grow for timber production since the spacing of a long-lived crop at harvest will be wider than at the time of establishment (Heimburger, 1962).

The process leading to the breakdown of resistant varieties is usually described in terms of the emergence of new virulent or adapted pathogen genotypes. In other words, failure is attributed to an unpredictable event. If we keep human behavior and facts about resistance in mind, we must suppose that many such "breakdowns" can be attributed to inadequate testing. For instance, nobody would talk about a breakdown of spring-frost resistance if a spruce variety that was never exposed to late frost failed the first time it was planted in a frost pocket. Unfortunately, the overall fraction of infected or killed individuals in a resistance test does not indicate the value of the testing method since this fraction depends on the genetic make-up of the host material, the environment, and the genotype of the inoculum. Different host varieties and individuals may become infected in different tests.

Selection for resistance solely in the field sometimes is insufficient because of the existence of more chance variation of escapes. The trees growing in the field could gain resistance because of their age and the

implied maturation of tissues at the infection court. Satisfaction cannot be derived from this condition since the offspring of these trees, if used for further breeding work, must pass through the most critical stage of their life cycle again. Artificial inoculation will have to be applied and we have heard about sophisticated equipment to test many small samples of trees for resistance. An important point here is that both quality and intensity of inoculation can be calibrated approximately (Bingham *et al.*, 1969). There are indications that variation of infection intensity can lead to inconsistent estimates of genetic variances and heritability and of tentative gain. Such estimates, particularly the latter, would diverge, and nobody would base all future operations on a single estimate. Without some idea of the order of magnitude of such estimates for several conditions, it is impossible to evaluate the prospects of various testing strategies.

Genetic correlations between various manifestations of resistance possess two aspects that may be considered in more detail. One is the correlation between early and adult behavior since in artificial inoculation one wants to have the host organisms small for easier handling. This means the host plants are younger (and also, in the case of blister rust, more liable to infection) and are exposed to an amount of infection that equals that of a longer period in the field. The other relates more to the infection as such. The test environments may be as different as the quality of the inoculum. Pathogenic races are almost invariably found in obligate parasites such as rusts. If the pathogen genotypes effective in the more or less heterogenous inoculum materials differ, the two measurements of resistance may be only loosely correlated because they measure different things. If the pathogen genotypes do not differ, one might expect that resistance under natural and artificial conditions measures the same thing and that only error variance is responsible for low correlations. Host vigor may affect the inference on genetic variation of host resistance quite drastically (Walker, 1966), since gene action depends on the environment in the broadest sense of the word.

It is clearly a matter of experimentation to find out which methods are efficient and to investigate whether several testing techniques should be used. One may wish to handle the various resistance measurements somewhat like a selection index by assigning equal weight to every such measurement. Fortunately, we deal with traits that are measurable relatively shortly after one another. On the other side, one might think of the higher selection differentials under some semi-natural, mass-screening procedure that the index cannot fully utilize. But it is not clear whether resistance *always* behaves like a quantitative trait with additive gene-effects prevailing. This method of selection may not be reasonable at all. Bingham *et al.* (1969) have described a way of planning and establishing tests that enables the breeder to make certain inferences about the population handled.

Both the measurement of the resistance reaction after inoculation and the mere observation of field resistance can be "biased" in some direction. We do not know which is more reliable, so we do best to accept both. This will lead to material with a broad genetic basis of resistance.

A prerequisite of persistence of an achieved degree of resistance is that the testing results show high repeatability over several physico-chemical environments and modes of exposure to infection. Otherwise the results may be simply artifacts in that the test conditions were in

some way extreme. The risk of a certain family or variety remaining basically untested is reduced by growing it under a series of environmental conditions. It is difficult to conclude whether something like geographic variation in virulence exists in the pathogen and whether the geographic pattern varies rapidly in time without major shifts in the genotypic structure of the host. If something of the sort exists, inoculation must employ pathogen samples from several locations - as was done here at Moscow. Or the host material must be exposed to the local pathogen at several locations within a given area. In the latter case artificial support of field infection might be difficult to accomplish. The method has the advantage that different host vigor in the various plantations (or sowings) is accounted for and more consistent estimates of general combining ability might be made. Thus, interaction variances between genotype and environment can be employed in estimating genetic gains that may be realizable in the area. The distribution of such experiments forming a series may greatly influence the validity of inferences made on success and persistence of various operations of resistance breeding.

"Absolute" resistance and its sooner or later breakdown are not encountered if the variation of resistance is quantitative and host material is exposed to other site conditions and pathogen genotypes. It is just the selection response that may diminish. Field resistance of half-sib families of *Pinus silvestris* against *Lophodermium pinastri* indicate that heritability for selecting trees on the basis of performance of their open-pollinated progenies is much lower if interactions with the environment are accounted for (Schmalenbeck Institute of Forest Genetics, Germany, *unpublished data*).

SUGGESTIONS

It is difficult to say anything under this heading without telling commonplaces to the gentlemen here at Moscow who just cannot do everything at the same time. The base material for breeding is most appropriately selected in areas where the pathogen wave went through and killed many individuals. This was done here. Since the mode of variation of resistance was not expected to be solely of the additive type, complete mating designs were employed preferably.

Species hybridization means to make a variety of new gene combinations available. But unlike agricultural resistance breeding where so often statements like "gene so and so from species so and so was incorporated in the new variety" are read, hybridization in forestry means an array of new problems. First of all, we must foresee what makes these other species resistant and how the genes responsible for resistance vary in the first few generations of hybrids. The environments of these new species may be different and the resistance behavior in hybrids of varying status may be rather sensitive in the new environment.

There should also be no fear of an intermittent generation of inbreeding like crossing full sibs or making backcrosses. Inbreeding is indicated in the selection for rare genes; but the mass-growing of inbreds is forbidden because their reduced growth and vigor may increase liability to infection.

Testing has to be done under as widely different conditions as required to sample all conditions where the varieties to be developed shall be grown in the future. This may teach us something about the

nature of the resistance involved and also means a more elegant, albeit more costly, way of finding resistant material than imposing heavy infection in only one test.

As it is hazardous to speculate on the future of resistant varieties, no predictions are attempted. The resistance breeders continuously observe their field tests in order to derive offspring-parent correlations, to keep an eye on the behavior of the disease, and to study the mode of increase in mortality. It might not be too alarming if at some later age a variety shows a sudden increase in mortality. In clonal seed orchards, for instance, it often can be observed that a few clones are killed by some endemic fungus that formerly deserved little interest. Whether an effect of counteraction in the pathogen is involved may be hard to prove. So, the recommendation may be given to study everything new right after it happens, not only to keep up with new virulence but to be one tree generation ahead. It must likewise be true with a sympatric and an introduced obligate parasite that, because of the length of the tree life (Heybroek, 1969), mass-growing, particularly of interim planting stock in pure stands, is self-destructive. One may argue whether also small experimental plantations exert troublesome selection pressure on the parasite population, but certainly the early release of varieties with anything but a broad basis of resistance may endanger the success of at least one generation of improvement.

CONCLUSION

I am impressed by the progress made in the project underway at Moscow. But I would pose these questions to Mr. Bingham concerning the outlook of this project. The 1969 paper (Bingham *et al.*, 1969) that was submitted in 1967 pointed out that the superiority of certain candidate offspring was likely to be underestimated. Does some new information exist on how much progress was obtained by the operations demonstrated here? How close was the eventual selection goal of much less than 100% healthy trees approached?

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FLOOR DISCUSSION

BINGHAM: May I try to reply, Hans, although I don't think I have any sort of complete answer. Are your questions aimed at field testing of the types that are there, and whether or not a different level of resistance persists?

HATTEMER: There was some talk about the difference in the general level of resistance between unselected and selected material, and there exists also some information upon the decrease of vulnerability with increasing age. Starting with the percentages we were told about yesterday afternoon, what further losses do you expect if you outplant this material into the field? I suppose the general level achieved so far is really close to the goal of the first step in selection for resistance before you take account of other characters.

BINGHAM: I would answer by saying that in the particular experiment at which we looked the level of inoculation there imposed was low. Perhaps it was more equivalent to field conditions than some experiments that were more heavily inoculated, for instance, those on the table that I handed out the other day. However, the only evidence we have that is of any consequence is that in our initial experiments, we outplanted trees directly to field plots. After 3 to 5 years on the field plots, trees surviving 1 or 2 artificial inoculations, plus 3 to 5 years exposure to fairly heavy natural inoculation from planted *Ribes*, were selected and potted. These trees were all run back through the artificial inoculation chambers before they went to the breeding arboretum where we store our long-range breeding materials. While we did manage to inoculate a certain proportion of these selected trees, most of them also survived artificial inoculation at ages 5-7. Also we gained back another increment of resistance, usually in bark types, which had not had a chance to express themselves previously. So it would seem that we can maintain this 25 to 30% level through 7 years at least. We simply haven't been able to manufacture enough of the F_1's to get them out for real field testing; however, they are in the nursery and the first planting will go in next year.

BLAIR: You mentioned something about inbreeding. I would like to ask if you or Dr. Stern would express any concern about going to a very small number of clones in an orchard, say four or five clones, as an intermediate measure in trying to get disease-resistant planting stock into the field. Would this, you feel, be an unwise step, assuming that we could get some resistance going this way?

HATTEMER: I was not thinking of a seed orchard but of controlled breeding work. In a seed orchard, you are never sure what really happens.

BLAIR: You must accept some of the inbreeding in the case where you have a small number of clones in a seed orchard, even though you don't know how much you are getting. Would you be concerned about it?

HATTEMER: I was referring to the particular situation that the project leaders are in. Parts of the distribution range were lost. So one has to do something, and inbreeding will occur anyway in nature, if man does not start planned breeding work.

SCHREINER: Hans, maybe I didn't quite follow you, but why do you think that field resistance must be reinforced with some type of inoculation research? Don't you think field resistance is a sufficiently good measure?

HATTEMER: I indicated, that in the field there is the risk of escapes. Trees we regard as resistant really are not. The second point is that we never have complete control over the genotype of the inoculum. It is virtually impossible in the field to figure out with which races our material was infected. It's real difficult to predict whether there exists something like geographic variation in *Cronartium ribicola* as it does seem to exist in other fungi which weren't introduced into this country. I mean we need a mutual backing up of the two test procedures.

BINGHAM: I would like to try to answer Roger Blair's question as I see it. Geral McDonald has helped us make some calculations of inbreeding coefficients in large full-sib families. Our calculations show very low values. For 10 families, the inbreeding was 2 percent in three generations or something like that. This certainly isn't much to worry about, Roger. I think what you should worry about is if you try to work within a confining population of this size, then you're hopelessly confined for variability in other traits.

BORLAUG: I would like to add one comment to this discussion that's been taking place the last few seconds. You narrow the base too much, and you lay yourself very vulnerable to secondary diseases that might have been of no significance in the past. Your genetic base has been greatly restricted, and you haven't paid any consideration whatsoever to this. I know that our maize (*Zea mays*) breeder, Ed Wellhausen, would die if he heard you talking about taking three individual plants out of a maize population and starting to propagate them, or use them as a base for breeding rust resistance. We would not worry about the rust, but some of the other diseases that are of no significance in populations as they exist now.

WEISSENBERG: It seems to me that the white pine resistance breeders now are in a situation where they will try to breed for a host population similar to the populations of *P. peuce* and *P. sylvestris* with respect to their associated rusts, *C. ribicola* and *Peridermium pini*. Here are two models. A system is functioning where the host and the pathogen are in some kind of equilibrium. I would like to hear Dr. Hattemer's comment on what we can learn from these systems and how to go about studying these systems. These types of systems seem to be the goal for the white pine breeders in North America, in other words, to achieve the model Mother Nature provides us with.

HATTEMER: I wouldn't give you any recipe on how many generations it takes for something to originate as it exists in the host-pathogen relationships that you were talking about. I have no comment whatsoever on this.

SCHREINER: On this matter of a balanced population, I would remind you that an introduced pest wiped out our native chestnut; there was never time to set up such bounds.

BORLAUG: I think this is a very good point. We don't live very long, and the way things are going now, time is pretty short.

GERHOLD: It would be interesting to know whether the balanced systems that have been mentioned started from a catastrophe, or whether they developed gradually with both host and pathogen evolving at similar rates.

BORLAUG: I might make a comment about a case of an equilibrium system that I think is more valid than any that has been proposed here and one that is truly in equilibrium. In maize rust in a center of origin of maize such as Mexico, it's no problem so long as you don't act foolishly and use too narrow a genetic base in trying to make other improvements. You never see an epidemic of maize rust in the open pollinated maize varieties, and it takes practically no toll as long as you don't move these varieties around or start inbreeding in them. I want to tell you this, don't believe there isn't variability just because you don't see it when you have this kind of system. You inbreed and a large percentage of these populations will be killed outright, in the same location where they are perfectly in balance. It will be more so if you bring a tropical maize race into a highland and start inbreeding it. These will fall apart even worse. When an organism, a virus in the case that I wish to cite, was introduced, it swept across Mexico from the North. It's now in Bolivia 20 years later. It had swept the maize varieties before and there was apparently a varying level of genes for resistance in these populations. But the disease was of such intensity that there was ruinous harvest or lack of it for about 2 to 3 years. Long before anyone ever figured out just what was happening, the peasant farmers, reselecting in these populations, solved the problem in Mexico. But it is still a problem in Bolivia as it advances. The virus is insect transmitted and it apparently came off a grass host growing in the Southern U.S.A. So, you have both extremes through a long period of time. As in the case of the two species of rust that are part and parcel with the maize system in the open populated varieties of Latin America in the mountainous country where they live together here, they cause practically no loss. The virus that came in was ruinous for two or three years and before the scientists could find out what was going on, the peasant farmers solved the problem. So let's not get oversized heads about what we can do and what we can't do.

ZADOKS: We were talking here about inoculation infection techniques. If I may make a few remarks. There are several choices to be made. One is the choice whether we should work with selected isolates which can be identified, or whether we work with populations of the pathogen. This is largely a matter of taste and of money. All sophisticated rust work in cereal breeding is with selected isolates, and a result of it was the well-known race between rust and breeder. The breeder just keeping in advance of the rust to get new varieties. I know of one country, Switzerland, which has kept its head cool and always worked with populations and has decided to continue to work with rust populations. Their argument was very simple. They said we had too little money to do all this work and to spend on this expensive equipment; so, they collected isolates from all over the country, mixed them to produce one big population, and infected their fields with this mixed population. They seem to go on quite nicely. Then another question about inoculation techniques is whether you should inoculate in inoculation chambers under controlled conditions to get rather severe inoculations, or whether you should leave the inoculations to the field. Here again it's a matter of taste and a matter of money. There are advantages in the laboratory techniques. You can select those strains or plants which are really resistant. The disadvantage is that you overdo the work, and kill most of the plants

which have some intermediate type of resistance. This has happened several times. The danger is, when you work in the laboratory, that you may select for major genes only. We have had breeders of onions who were selecting for *Botritis* resistance. They complained to me that they never could get any resistance but it just should be there in the material. I asked them about their inoculation technique. Well, they did it in the laboratory. After additional questioning, I concluded that they far overdid the work. They killed everything outright just by too heavy a dosage of inoculum and too good conditions for infection. I think for tree breeding, controlled inoculation is just not necessary if you can increase the average of resistance in a population without it. You have done already a lot of work and I believe the increase in resistance could be done in the field using natural infection.

HATTEMER: Your first question was on the problem of isolates versus "populations". If you can be sure that the quantity of spores you use for inoculation contains all races of the pathogen in proportions that reflect the future risk of field infection you can of course save money. If this is not the case you can do nothing but investigate the genetic variation of the pathogen, test host resistance against isolates or just various samples of the pathogen population, and make periodical surveys of the race spectrum that occurs in the field. You may also know that Idaho alone is many times larger than Switzerland and this may have an enormous impact on whether the Swiss approach works for white pine. You just have to realize what you are working with, that your final goal is minimum loss at the age of maturity, and the same I think is true with the question of testing after artificial versus natural inoculation. If you can be sure one or the other or maybe both have a close enough correlation to the goal of the resistance breeder, you can make the choice. The third problem is that of killing possibly the most valuable selection material. We have, of course, to be aware of the fact that we should not overkill. There are various breeders, not only of trees, who have been unsuccessful for years and years because they have virtually extinguished all the material that they had in their garden.

MASS PRODUCTION OF IMPROVED FOREST TREE PLANTING STOCK THROUGH SYNTHETIC VARIETIES

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ABSTRACT

Mass breeding methods for multiple-trait improvement of forest planting stock are discussed, with emphasis on rust resistance in *Pinus*. Varieties with super, overall genetic fitness are a good objective, but will require both populational and individual buffering.

Advantages and disadvantages of (1) single- or multiple-cross hybrids, (2) varietal blends, (3) multilineal varieties, (4) synthetic varieties, and (5) multiclonal hybrid varieties for mass production of improved planting stock are discussed.

INTRODUCTION

This paper is an attempt to evaluate mass breeding methods for multiple-trait improvement of forest planting stock with emphasis on pest resistance, particularly rust resistance in *Pinus*. Practically all forest tree species need improvement in more than one trait. For example, rust resistance in *Pinus strobus* L. would be of very little value in the Northeastern Region without white pine weevil resistance and rapid growth; and for upland planting of rapid-growing hybrid poplars, rust resistance without a wide range in site adaptability would have very limited practical value.

BREEDING FOR FITNESS IN FOREST TREES

The overall object of forest tree breeding should be the creation of varieties with a high degree of fitness. Fitness is generally defined as the relative ability of an organism to survive and transmit its genes to the next generation (King, 1968), and variability in fitness is defined as the variability under different environments (Pfahler, 1964). Adaptability to the widest possible environmental variation, including field resistance to diseases and insects, will require well-buffered varieties with a broad adaptive norm.

BUFFERING BY GENETIC DIVERSIFICATION

Jensen (1952) cites the practice of growing mixed crops of oats and barley and, occasionally, oats, barley, and spring wheat in some northeastern states. He suggests that the feature of stability found in crop mixtures has played some part in the persistence of this agricultural practice, often without benefit of scientific approval. Suneson (1960) emphasized the buffering effects of genetic diversification on crop pests, with examples of the nonuniform crop varieties, Coast barley, Red Rustproof oats, and Kherson oats, which had survived the vicissitudes of diseases and insects for many years with only partial damage.

Allard and Bradshaw (1964) discussed the implications of genotype-environmental reactions in applied plant breeding. They noted that the stability with which we are concerned does not imply general constancy of phenotype in varying environments; it implies stability of economically important traits. They suggested populational buffering as one approach in that varietal stability can be achieved by constituting a variety with a number of genotypes each adapted to a somewhat different range of environments. Genetically homogeneous populations, such as pure-line varieties or single crosses, obviously depend heavily on individual buffering so that each member of the population is well adapted to a range of environment. Both paths are open to genetically heterogeneous populations. Although there is widespread use of population buffering in corn through the use of genetically heterogeneous double-cross hybrids, Allard and Bradshaw suggested that other types of populations seem feasible, including deliberately compounded mixtures of single crosses, mixtures of double crosses, and synthetic varieties.

CHROMOSOMAL AND NONCHROMOSOMAL INHERITANCE

Jones (1960) pointed out the necessity for extending genetic terminology to include both chromosomal and nonchromosomal hereditary material. He suggested the terms "plasmatype" and "chromotype," respectively, for the two major components of the units of hereditary transmission that make up the genotype. The possible role of the plasmatype must not be overlooked in breeding for forest tree improvement. There should be a conscious effort to bring together the plasmatype and chromotype that will give the most efficient genotype.

Cytoplasmic inheritance of resistance to a needle blight of European larch has been reported by Langner (1951/1952). In corn, Fleming, Kozelnicky, and Browne (1960) obtained significant cytoplasmic effects for silking, ear height, plant height, erect plants, yield, and budworm damage. They found that a significant cytoplasmic difference which occurs one year in a given environment may not occur in another year under a different environment. Hunter and Gamble (1968) reported yield differences as great as 565 kg of shelled corn per hectare between hybrids differing in cytoplasmic source. Nagaich *et al.* (1968) have published apparently the first report of cytoplasmic control of infection types involving a virus.

The use of cytoplasmic male sterility and the restoration of fertility is being used more and more extensively in crop breeding, and it undoubtedly will be useful in forest tree breeding. Natural mutations have been the usual source of male-sterile genotypes. However, Erichsen and Ross (1963) found that the colchicine-induced mutants in sorghum with

the most striking abnormalities were cytoplasmic male-sterile. From cytological study of the abnormalities, they concluded that the mutants had the same or a similar mechanism causing male sterility as that being used in the production of hybrid sorghum.

BREEDING FOR RUST RESISTANCE IN *PINUS*

The objective of pest-resistance improvement should be to select or breed trees that have sufficient resistance to provide a profitable harvest. Since resistance to pests is seldom absolute, it is necessary to set up minimum standards of field resistance acceptable in practice for each host-pest relationship. For biologic and economic reasons, these standards must be flexible in time and place (Schreiner, 1960).

Field resistance differs from immunity or hypersensitivity in that it is under the control of many gene loci. Polygenic control is believed to be responsible for the greater stability of field resistance because several mutations in the parasite may be necessary to overcome this type of resistance (Williams, 1964, p. 422).

A few brief remarks on breeding methods are needed as a preface to mass production of rust-resistant pines. Maximum improvement to combine rust resistance with other commercially essential traits will require: (1) Establishment of broad-base gene pools; (2) extensive phenotypic selection in natural populations (and eventually in gene pools); (3) large-scale progeny testing; (4) recurrent selection; (5) intraspecific breeding, including selfing and backcrossing; and (6) species hybridization.

My suggestions for the establishment of broad-base gene pools have been published (Schreiner, 1968), and there is now general acceptance of the need for phenotypic (plus tree) selection.

RECURRENT SELECTION

Recurrent selection has been defined as "A breeding system involving repeated cycles of selection and recombination with the objective of increasing the frequency of favorable genes for yield or other characteristics." Recurrent reciprocal selection is "A recurrent selection breeding system in which two or more geneticlaly divergent groups are maintained and selections from each group are tested for combining ability with the other group or groups in each cycle" (Leonard, Love, and Heath, 1968).

There has been considerable variation in the operational procedure for recurrent selection. In corn breeding, plants selected from a heterozygous source are self-pollinated and are evaluated for some desirable trait or traits. Progenies of the superior plants are propagated from the selfed seed and all possible intercrosses among these superior progenies are made by hand or by top-cross or poly-cross methods. The resulting population serves as source material for additional cycles of selection and intercrossing (Allard, 1960).

Penny, Scott, and Guthrie (1967) reported that, in their recurrent selection for leaf-feeding resistance to the European corn borer in five synthetic varieties, two cycles of selection were sufficient to shift the

frequencies of resistance genes to a high level in all varieties. Three cycles produced essentially borer-resistant varieties. The general procedure for this work was to self-pollinate individuals in a segregating population, evaluate the S_1 lines, and intercross a selected sample of these S_1 lines to provide the new base population.

Paterniani (1967) has used a modified ear-to-row selection procedure in maize (selection among and within half-sib families) that he concludes is superior to recurrent selection for general combining ability. Open-pollinated progenies were evaluated in replicated field trials, and the selected half-sib families were subjected to mass selection within families to provide the half-sibs for testing in the next generation. Yield improvement of 13.6 percent per cycle compared to the original population was obtained in three cycles of selection.

From the theoretical standpoint, the Monte Carlo computer simulation by Cress (1967) on reciprocal recurrent selection and modifications in a bisexual organism with two allels at each of 40 independently segregating loci may be of interest. He concluded that two points seem essential to all recurrent selection systems in order that both maximum genetic potential and rapid progress are possible:

> "(1) All genetic material entered into a long term program of selection with progeny testing should be combined into one synthetic population. Any subsequent populations required would be obtained by sampling this synthetic. This procedure reduces the problem of multiple alleles and can only increase not reduce the genetic potential."
>
> "(2) One generation of selfing (or inbreeding) should precede the test cross, where the real time lapse measured against rate of progress shows this to be more efficient."

For improvement of perennial forage crops, the usual procedure is phenotypic selection of clones for polycross tests for general combining ability. Syn-0 parents for each cycle of selection and intercrossing are then selected on the basis of the performance of the polycross progenies.

LARGE-SCALE PROGENY TESTING

Large-scale progeny tests are feasible for blister rust resistance. Bingham (1968) has shown that mixtures of 10 or more pollens can be used to obtain relatively reliable estimates of general combining ability and breeding value of blister rust-resistant plus trees. In 95 out of 100 cases, the results fell within ±3 percent of those obtained by using 4 individual tester crosses. This level of accuracy is adequate for large-scale practical testing, but Bingham also noted that prevention of patchy inoculation of test plots, as well as an increase in the number of progeny test plots, would further improve accuracy.

INTRASPECIFIC BREEDING

Selfing

Selfing will be difficult in some, but not all, *Pinus* species. On the basis of close observation of 45 *Pinus monticola* Dougl. trees for periods up to 6 years, Bingham and Squillace (1957) concluded that no phenological barriers to either selfing or crossing existed in the trees under observation. Barnes (1964) reported growth depression from selfing in *Pinus monticola*, but also highly self-compatible individuals.

Snyder (1968) is of the opinion that inbreeding will not be practical in *Pinus elliottii* Engelm.; among 35 trees, 80 percent produced less than one seedling per self-pollinated flower. He concluded that "...until quicker methods for obtaining homozygous diploids are developed, results from such a system can probably be surpassed by crossing." His opinion was based on the need for two or three generations of selfing followed by the combination of the final lines into F_1's by another generation of breeding.

One generation of selfing followed by a progeny test is usually sufficient for recurrent selection and for the selection of parents for the establishment of a basic (Syn-0 generation) breeding population for production of a synthetic variety. It is true that homozygosity through selfing or inbreeding is never accomplished in a single step by breeding. In fact it is probable that the complete homozygote can only be obtained by diploidization of a haploid. This would be possible in a short one-step or, at most, two-step process.

Niizeki and Oono (1968) have produced haploid rice plants from immature pollen grains by culturing anthers on an agar medium about 5 days before anthesis. Hundreds of haploid plants of various species of *Nicotiana* have been produced from cultures of pollen grains by Nitsch and Nitsch (1969). Their method is based on the stimulation of cell division in immature pollen grains to produce plants from the male prothallus.

There is increasing interest and research on the production of haploids and their diploidization in forest trees. The role of haploids in tree improvement and forest genetics has been reviewed by Kopecky (1960), Nei (1963), and Stettler (1966). Stettler (personal communication) has reported "successful experimental induction of haploid parthenogenesis..." in *Populus trichocarpa* Hook. Winton and Einspahr (1968) have reported on the possible production of aspen haploids using pollen weakened by heat. They note that the recovery of spindly diploid aberrants, as well as glaucous diploids from *Populus tremuloides* Michx. x *Populus alba* L. indicates that spontaneous diploidization occurred in maternal haploids. F. A. Valentine (personal communication) has obtained spontaneous diploidization of a monoploid *Populus tremuloides*.

Backcross Breeding

Backcrossing is highly effective for transferring one or two simply inherited characters to an otherwise desirable type. According to Briggs and Allard (1953):

> "The use of recurrent backcrossing for improving crops in characters dependent on numerous genes is limited only by the ability of the plant breeder to select for a worthwhile intensity of the character. This is the chief limiation in dealing with such characters, regardless of the method employed. In order not to dissipate the desired genes, each backcross must be followed by rigid selection."

SOURCES OF INTRASPECIFIC RESISTANCE

White Pines

The current breeding programs (listed by Bingham *et al.*, 1969) aimed at mass production of partially blister rust resistant types of *Pinus strobus*, *P. monticola*, and *P. lambertiana* Dougl. are based on sound evidence for sufficient natural resistance to warrant such programs. On the basis of their research with *P. monticola*, Bingham *et al.* (1969) have predicted an expected gain of 4.3 to 7.1 percent, 8.5 to 19.9 percent, and 9.9 to 23.7 percent, from Stage A, B, and C clonal seed orchards, respectively.

Southern Pines

Barber (1966) found highly significant differences in fusiform rust infection among half-sib families from three *Pinus taeda* L. stands in Georgia. There was a ninefold increase in rust-free trees in the best progeny as compared with the poorest; some of the fastest growing families were among the more resistant to fusiform rust. Jewell and Mallett (1967) have concluded from controlled pollinations among and between rust-free and rust-infected selection of *P. elliottii* Engelm.:

> "...that resistance and susceptibility are under strong genetic control and are transmissable. Thus geneticists can plan a breeding program for general tree improvement and can implement it by selecting rust-free parents..."

INTERSPECIFIC HYBRIDIZATION

White Pines

Bingham (1961) has made a strong case for intraspecific breeding as a rapid and safe means to meet the immediate need for resistant planting stock. But he adds that, ultimately, it probably will be necessary to incorporate resistance factors from other species, and that "A common-sense approach is to carry separate lines of resistant inter-species hybrids, meanwhile selecting for adaptations while slowly incorporating them in the over-all breeding scheme." Callaham (1962) has suggested that hybrids of *P. strobus* x *Pinus wallichiana* A.B. Jacks. should be subjected to further investigation, and that the rust resistance of hybrids involving *P. monticola*, *P. strobus*, and *P. wallichiana* could be enhanced by using parents selected for good general combining ability for resistance. Heimburger (1962) and Patton (1966) have shown that it is possible to introduce into *Pinus strobus* factors for blister rust resistance from less-susceptible related species such as *P. wallichiana*, *Pinus parviflora* Sieb. & Zucc., and *Pinus peuce* Griseb.

Southern Pines

There is sufficient individual resistance to fusiform rust in *P. taeda* and *P. elliottii* to justify intraspecific breeding. It is doubtful, however, whether the gain to be expected from intraspecific breeding would be as great as might be expected from species hybridization.

Pinus echinata Mill. x *P. elliottii* and *P. echinata* x *P. taeda* F_1 hybrids are highly resistant under natural exposure. The Southern Institute of Forest Genetics and the U.S. National Forests in the Southern Region have a cooperative program to produce the *P. echinata* x *P. elliottii* hybrid in quantity for planting on National Forest areas where rust incidence is high (Henry and Jewell, 1963).

Although the *P. echinata* x *P. elliottii* hybrid is very promising, Snyder and Squillace (Quoted by Wakely, Wells, and Campbell, 1966) reported that seed yields from controlled pollinations averaged only 8.5 sound seeds per cone. Wakeley *et al.* (1966) tried a simple method for mass-producing this hybrid by dusting a mixture of *P. elliottii* pollen in large quantities on unbagged *P. echinata* flowers. An average of 10.7 percent of the seedlings resulting from such mass-pollination showed definite evidence of hybridity. They concluded that, if mass-pollinations were carried out only the high hybrid-yielding trees (which yielded 20 percent hybrid progeny), the technique would be more economical than controlled pollination.

Pinus palustris Mill. x *P. elliottii* hybrids planted in central Louisiana are demonstrating desirable characteristics of both parent species. They closely resemble *P. palustris* in form and branching habits, but start height growth immediately and grow almost as fast as *P. elliottii*. They appear less susceptible than their parents to the brown spot needle blight of *P. palustris* and the fusiform rust of *P. elliottii* (Derr, 1966).

MASS PRODUCTION OF RUST-RESISTANT PLANTING STOCK

The eventual commercial production of planting stock may be by any or all of the following procedures: (1) Single- or multiple-cross hybrids; (2) varietal blends; (3) multilineal varieties; (4) synthetic varieties; (5) multiclonal varieties.

SINGLE- OR MULTIPLE-CROSS HYBRIDS

The evidence from crop breeding indicates that the best F_1 single- or double-cross hybrids are generally superior to synthetic varieties. The use of synthetics stemmed from the difficulties and cost of producing hybrid seed or from the susceptibility of pure lines or F_1 hybrids to inimical environmental factors, particularly disease and insect infestation.

The availability of practical methods for the production and diploidization of haploids and/or of natural or induced cytoplasmic male sterility in forest trees would open new avenues for improvement breeding through intra- and interspecific hybridization. For additional populational buffering, hybrids could be used in varietal seed blends or in multiclonal hybrid varieties.

VARIETAL BLENDS

The evidence from crop plants indicates that increased population buffering to enhance environmental adaptability of mass-produced, rust-resistant hybrid or synthetic varieties of forest trees could be obtained through seed blends.

Probst (1957) reported performance studies on 3 varieties of soybeans grown separately and on 13 different blends of these 3 varieties. The blends were not superior in yield over the highest yielding variety, but there was a marked variety x season interaction. In this respect, blending had a stabilizing effect on yield and appeared to be of importance in approaching maximum yield each year.

Browning (1957) grew 2 varieties of oats (one susceptible and the other resistant to race 7 of the stem rust fungus) in pure stands and in 50-50 mixtures subjected to an induced epiphytotic of race 7. In 2 successive years, the yield of the mixture was above the average of the yields of the component varieties grown in pure stands, and much less rust developed on the susceptible variety in the field blend.

Patterson *et al.* (1963) compared 6 varieties of oats in pure stands and in equal blends of the 6 in all combinations of 2 for 4 years. Improvement from breeding with parental varieties similar to those compared in the blends greatly exceeded improvement from the blends; they concluded that blends may provide a useful interim improvement.

Pfahler (1964) studied the fitness of 6 homogeneous varieties of *Avena* and a heterogeneous composite of all 6 varieties. Differences between the varieties were significant at the 1 percent level; the fitness of the composite exceeded the mean of the 6 varieties.

MULTILINEAL VARIETIES

Pure-line breeding has been the almost exclusive procedure for the improvement of self-pollinating crop plants. Rust-resistant varieties (lines) of wheat and oats have been developed, but the average maximum duration of effective protection by a particular type of resistance in wheat has been about 15 years (Borlaug, 1966); in oats, Sprague (1967) estimates that the average useful life of a new rust-resistant variety has been about 5 years.

Jensen (1952) discussed the possibilities for producing a satisfactory multiline variety of oats through a seed blend of pure lines, because such a multiline variety could be expected to possess a longer varietal life, greater stability of production, broader adaptation to environment, and greater protection against disease. The basic assumption in the design of a multiline variety was that the chance for maximum production is subordinated to the principle of stability; and that this feature of stability is always pointed toward a future risk situation, primarily the risk of a disease epidemic.

Borlaug (1953) and Borlaug and Gibler (1953) proposed the production of a "composite variety" of wheat by a modification of conventional backcross methods. The "backcross lines" would be developed by crossing a commercial variety to a number of varieties having different types of resistance. The several lines would be multiplied separately and mixed

mechanically to form the variety for release to seed growers. Borlaug (1966) reported that multilineal varieties of wheat had been developed by the Mexican and Colombian wheat programs. He also described the possibilities for incorporating more lasting rust resistance into wheat through the development of multilineal hybrid varieties by the use of recently found cytoplasmic sterility systems and fertility restorers.

Sprague (1967) agreed that a mechanical mixture of morphologically similar substrains, each possessing resistance to one or more of the prevalent races of rust, would insure a less rapid buildup of new rust biotypes. He states that, "although this procedure has not been fully evaluated, preliminary evidence indicates some measure of effectiveness."

The use of seed blends, analogous to multilineal varieties of rust-resistant cereals, must await the development of practical methods for the production of rust-resistant lines of forest trees. Furthermore, the development of lines resistant to particular races of the rust will not be possible until races of tree rusts have been identified. New races of rust would not be expected to develop until there are extensive plantations of a rust-resistant variety.

SYNTHETIC VARIETIES

The product of forest tree seed orchards will be synthetic varieties basically analogous to those developed for outbreeding agricultural crops.

A synthetic variety can be defined as the "Advanced generation progenies of a number of clones or lines (or of hybrids among them) obtained by open pollination" (Leonard, Love, and Heath, 1968). Allard (1960) has defined the general concept of a synthetic variety in more detail:

> "A synthetic variety is one that has been synthesized from all possible intercrosses among a number of selected genotypes; thereby a population is obtained that is propagated subsequently from open-pollinated seed. The essential difference between a variety developed by mass selection and a synthetic variety hinges on the way in which the genotypes to be compounded into the new variety are selected. In mass selection, the next generation is propagated from a composite of the seed from phenotypically desirable plants selected from the source population. A synthetic variety is made up of genotypes which have previously been tested for their ability to produce superior progeny when crossed in all combinations. Also, in mass selection, the male gametes represent a, more or less, random sample from the entire previous generation, whereas, in a synthetic variety, pollination is controlled so that the gene frequencies of the selected materials is maintained in the male as well as in the female lineage."

Sprague and Jenkins (1943) defined a multiple cross as the first generation of a cross containing more than four inbred lines and a synthetic variety as the advanced generations of such a combination maintained by mass selection.

There is considerable diversity of evidence (and opinion) on the breeding procedure and performance of agricultural synthetics, particularly of maize and forage crops.

Synthetic Varieties of Maize

As early as 1919, Hayes and Garber suggested "synthetic production of a variety by self-fertilization, crossing, and subsequent selection" as one of three possible means of utilizing increased vigor from crosses (Hayes and Garber, 1919). They recognized that:

> "...before combining selfed lines for the purpose of producing improved varieties, it is necessary to determine the yielding ability of all F_1 combinations. Selfed lines which combine favorably with all others that are to be used should then be used for the recombinations."

Hayes (1926) also was one of the earliest breeders to report research with synthetic corn varieties. He recombined selfed strains selected for yield by pollinating several plants in each strain of a variety with a mixture of pollen from other strains of the same variety. Yields of five synthetics, each made up of lines derived from a single commercial variety, ranged from -11.7 to +16.6 percent of the parental varieties from which they were derived. Hayes concluded that it might be difficult to obtain a variety that will be as vigorous as certain F_1 crosses, but he did predict that "...if resistance to some particular disease is a major importance and resistant lines can be obtained, there is every reason to expect that improved synthetics can be secured.

Sprague and Jenkins (1943) presented data on the performance of 5 synthetic varieties and 16-line multiple crosses. The synthetic varieties gave approximately the same yield as adapted open-pollinated varieties. Multiple crosses compared favorably with available standard double crosses. Hayes, Rinke, and Tsiang (1944) produced a synthetic variety from 8 inbred lines that represented rather wide genetic diversity and gave relatively satisfactory performance in all single-cross combinations with each other. The synthetic was almost equal to Minhybrid 403, and both the synthetic and Minhybrid were greatly superior to open-pollinated varieties.

In the opinion of Lonnquist and McGill (1956), the general conclusion derived from earlier synthetic varieties, that they were little better than commonly-grown open-pollinated varieties, was probably due to the fact that the component lines used in such synthetics were not chosen for their combining ability. They concluded from their own research that synthetic varieties of corn produced by intercrossing selected S_1 lines of high combining ability, as determined in top-cross combinations, can be expected to maintain their improved productivity in advanced generations through normal mass-selection procedures. Yields of 4 second-cycle synthetics averaged 96 percent of hybrid U.S. 13 in yield, as compared with 82 percent for the first-cycle populations, over a 2-year period of testing.

Wernham (1960) has discussed the uses and advantages of disease-resistant synthetics of maize with particular emphasis on the method used to acquire the adaptability of local varieties and maintain the resistance of the original synthetic. According to Hallauer and Eberhart (1966), synthetic corn varieties have been used extensively in recent years as populations for the extraction of selection lines. The main objective has been to increase the gene frequency for specific attributes because higher frequency of either better or more desirable genotypes would be expected in these synthetic varieties.

Synthetic Varieties of Forage Crops

There has been considerable diversity of opinion on the procedure for, and the improvement possible through the development of synthetic forage varieties.

The Ranger variety was the first synthetic alfalfa variety registered (1944) by the Committee on Varietal Standardization and Registration of the American Society of Agronomy. According to Kehr (1959), the major objectives in the breeding of this synthetic were to develop a winter-hardy and, particularly, a bacterial wilt-resistant variety. The original base populations from which the first selections were made were from 3 varieties (Cossack, Turkistan, Ladak) from widely separated provenances--Russia, Turkistan, and India. Five strains (synthetics that had been developed by selfing, out-crossing with wilt-resistant lines, and isolated increase) were blended in prescribed proportions for the Syn-0 generation breeder seed. On this base population, the Syn-1, Syn-2, and Syn-3 were produced for foundation, registered, and certified seed, respectively. As of 1959, more than 200 million pounds of certified seed of this variety had been produced and planted since its release. Kehr also noted that, "Taking into consideration the many factors which influence wilt test results, it was concluded that the wilt reaction of Ranger has been sufficiently constant so that field performance has not been altered since the variety was released."

Pearson and Elling (1960) concluded that varieties of alfalfa superior in wilt resistance and common leafspot resistance can be produced by combining clones of superior general combining ability for these characteristics. Their experimental results indicated that synthetic variety performance essentially agreed with the average performance of all the crosses among the clones of which each synthetic was composed.

Kehr *et al.* (1961a) found great variability in the forage yield performance of four generations of individual alfalfa synthetics. Factors which may contribute to performance as generations are advanced include relationship of parental clones, method of producing the Syn-1 generation, fertility and compatibility relationships, natural selection, genotype and environmental interaction in both seed and forage production, age and quality of seed, and sampling error.

On the basis of their study of forage yields of the Syn-1 generation of 4-clone synthetics produced by using the Syn-1, Syn-2, Syn-3, and Syn-4 generations of parental two-clone synthetics, Kehr, Lowe, and Graumann (1961b) suggested commercial production of Syn-1 generation synthetics until the necessary genotypes are available for commercial production of true hybrid alfalfa by controlled crossing. Pearson and Elling (1961) also suggested that the clonal crosses of highly selected alfalfa clones would be more desirable than combinations of clones as synthetic varieties.

Theurer and Elling (1963) evaluated the 10 single crosses, 26 possible Syn-2 generation synthetics, and the S_1 progenies of 5 alfalfa clones for resistance to bacterial wilt. The best single cross was not significantly more resistant than the better synthetic varieties. In a subsequent paper (Theurer and Elling, 1964), they reported the forage yield performance of the same single crosses and Syn-2 synthetics. Synthetics developed from a larger number of clones tended to yield the most forage in Syn-2. One or more single crosses surpassed the yield of the best synthetic each year, but the differences were in no case significant. They noted that their

results were contrary to research by other workers who found substantial gains of single-cross over synthetic yields.

Craigmiles, Crowder, and Newton (1965) compared the yield of F_1 bromegrass hybrids (produced by isolating vegetative material of 2 self-incompatible but cross-compatible clones), 2 experimental 6-clone synthetics, and the commercial variety, Southland. The F_1 hybrid was the most productive, with an increase of 20 percent over Southland and 15.8 percent over the best synthetic tested. The synthetics were not significantly better than Southland, the highest-yielding variety previously tested. Christie (1967) has recorded serious doubt as to the value of synthetics:

> "Forage crop breeders have become increasingly concerned over the lack of an increase in yield per se as a result of breeding. Improvements have been made in such traits as winter-hardiness, leafiness, disease resistance, and chemical composition, but the increase in yield of dry matter has been disappointing....At present, most breeders select clones on the basis of phenotype, evaluate for combining ability, and then use the superior clones as the basis of a synthetic variety. In theory, this seems to be a promising method. Since progress has been disappointing, why don't the results confirm the theory? It is becoming increasingly obvious that one possible weakness in present forage breeding is the assumption of random pollination....There are other possible reasons which it is hoped will be reviewed at a later date."

Synthetic Varieties of Forest Trees

Selfing is necessary with annual crops, such as maize, to maintain the strains (homozygous lines) used for the parental Syn-0 generation; selfing is not necessary with forage crops or forest trees where the parental Syn-0 plants can be maintained as clones. Synthetics of alfalfa and other perennial forage crops have been developed by intercrossing noninbred plants without control of pollination except for restricting parentage in number and by isolation (Kehr *et al.*, 1961b). This procedure will apply also to the production of synthetic varieties of forest trees. Also, as with forest trees, the production of synthetics has been favored because of the difficulty of large-scale controlled crossing for the production of hybrids for commercial use. For the same reason, open-pollinated progeny tests, top-cross tests, and polycross tests have been generally utilized to obtain progenies required for tests of combining ability.

Clonal and seedling seed orchards are the base populations--the Syn-0 generations--for the production of synthetic varieties. The planting stock obtained from seed orchards before they have been progeny tested and rogued for general combining ability should be recognized as the first generation product of mass selection.

The open-pollinated progenies of the orchards after roguing will be Syn-1 synthetics. Seed-increase to produce Syn-2 foundation seed, and Syn-3 certified or registered seed (as in agricultural crops) is neither practical nor anticipated for forest trees. Seed orchards are generally large enough to meet the forestation requirements of the organizations that establish them. A succession of seed orchards, for example, as in Bingham *et al.* (1969) Stage A, Stage B, and Stage C orchards, established

with selected high-GCA candidates from each preceding stage, would each be the Syn-0 generation for new Syn-1 synthetics.

Progeny test methods, using controlled pollinations with individual male testers or pollen mixtures, are practical and have been developed for clonal seed orchards. Seedling seed orchards are also half-sib progeny tests and should be designed as such. They would be rogued to leave the best individuals of the best progenies. The planting stock produced after the first roguing would be a "mass-selection" synthetic; theoretically, with a broader genetic base and wider cryptic variability than the Syn-1 from a clonal orchard composed of a relatively small number of clones.

The evidence from crop breeding on the effect of the number of individual genotypes in the Syn-0 generation is based largely on the performance of later than Syn-1 generation synthetics because of the need for seed-increase. The effect of the number of Syn-0 genotypes on the Syn-1 generation of wild forest tree species is an open question. Syn-1 synthetics may be different from year to year; each year will provide possibilities for variation in the pollination pattern and the individual seed productivity of individual trees. This will be reflected in a variation of the genotypes present in the synthetic variety in different years. Therefore it will be advisable to label the production of seed orchards by "vintage" years.

MULTICLONAL HYBRID VARIETIES

During the past 30 years, I have emphasized the importance of the clone for forest tree improvement, the need to develop practical methods for economical asexual propagation and, in recent years, my conviction that maximum genetic improvement will be achieved and maintained through multiclonal hybrid varieties (Schreiner, 1939, 1958, 1960, 1963a, 1963b, 1966a, 1966b, 1967).

A multiclonal hybrid variety would be a mixture of many hybrid clones (intra- or interspecific hybrids, or both) selected for a high degree of vegetative fitness and for important special traits such as resistance to pests. In the case of hybrid poplars, the availability of exceptionally superior clones has resulted in very extensive monoclonal cultures. The hazards of monoclonal cultures of forest trees have been pointed out, independently, by Hartley (1939) and by Schreiner (1939), and in recent years by a few other writers.

The use of multiclonal varieties requires economically feasible methods for asexual propagation of superior genotypes; at present, very few forest species can be vegetatively propagated for commercial forestation. Since basic research on vegetative propagation of forest trees is now well underway and increasing, I believe practical methods for clonal propagation of important but difficult-to-root forest species will become available within the next decade. Winton (1968) has produced complete plantlets in tissue culture from callus of a triploid *Populus tremuloides*. Wolter (1968) has controlled root and shoot formation in callus cultures of *Populus tremuloides* with auxin (NAA) and cytokinin (BAP), respectively. Brown and Lawrence (1968) are currently growing callus cultures of *Pinus palustris*, *P. taeda*, *P. elliotti*, and of *Thuja*, *Larix*, and *Picea* species to investigate the factors involved in propagating difficult-to-root species.

The average genetic improvement of all the progenies (full-sib or half-sib) represented in the mass-produced planting stock derived by seed from improved varieties--single- or multiple-cross hybrids, multilineals, or synthetics--will determine the genetic gain. Therefore, genetic improvement of such varieties will require parental populations with high general combining ability, not only for special traits but also for a high degree of fitness. How long will it take to create a "practically" true-breeding variety of *Pinus strobus* that combines a reasonably high degree of fitness with blister rust resistance, white pine weevil resistance, rapid growth, and good timber quality? 50 years? 100 years? And how long could it be maintained without alteration?

Exceptionally superior individuals may be obtained by various intensive breeding methods, or by extensive selection in progenies derived from gene pools or natural populations. Patton and Riker (1966) found that rust-free *Pinus strobus* ortets selected in natural stands showed a broad range of susceptibility in clonal tests, from high resistance (if not immunity) to extreme susceptibility.

Multiclonal varieties will depend upon the *selection of individuals* for a high degree of inherent fitness and desired inherent attributes, *not on the average inherent performance of families or lines*. When individual clones in a multiclonal hybrid variety begin to lose their value, due to increasing disease or insect susceptibility, lack of local adaptability, decline of general fitness resulting from long-term environmental changes, or to change in industrial use requirements, they could be replaced by new clones selected from the appropriate regional gene pool. Such clonal changes could be made on short notice because the breeder could multiply superior genotypes for commercial use *without adulteration of the genotype, and without determining their combining ability to transmit the desirable qualities or characteristics*. Seed orchards and progeny test plantations will provide unusually extensive and diverse gene pools for the selection of ortets for clonal testing for use in multiclonal hybrid varieties.

The breeding procedure to obtain multiclonal hybrid varieties should follow the same general pattern of selective intraspecific breeding, including sib- and backcrosses, species hybridization, and recurrent selection as for the development of synthetic varieties to be propagated by seed; but there should be a difference in the nursery procedure and the progeny tests. As large a number of selected seedlings as possible (F_1 and later generations) should be released from competition and grown in the nursery beds or, preferably, in a transplant nursery long enough to produce a sufficient number of ramets for replication of *at least* 2-tree clonal plots in several regional progeny tests. This would increase the size of the progeny test plantations, but they would then also be clonal tests, and by proper roguing, gene pools of superior genotypes. The clonal tests would be the source of superior clones for use in multiclonal hybrid varieties and for continuing individual- and mass-pedigree breeding.

Depending on the growth rate and reproductive habit of the species, the inherent characteristics or qualities to be improved, and assuming the availability of a sufficient number of parent trees, the total time required to complete one breeding cycle in the production of synthetic seed varieties, and to produce first-cycle ortets for mass propagation in multiclonal hybrid varieties might be approximately as follows (Schreiner, 1966a,b):

For completion of one breeding cycle.....10 to 26 years

(Selection of parents for the first controlled sibbing, backcrossing, or mass-pedigree breeding)

To provide first-cycle tested ortets.....10 to 24 years

(For multiplication for use in multiclonal hybrid varieties)

SUMMARY

The overall objective of mass breeding methods for multiple-trait improvement of forest planting stock with emphasis on pest resistance should be the creation of varieties with superior genetic fitness. This will require both populational and individual buffering.

Mass production of improved planting stock may be by any or all of the following procedures: (1) Single- or multiple-cross hybrids; (2) varietal blends; (3) multilineal varieties; (4) synthetic varieties; (5) multiclonal varieties.

The evidence from crop breeding indicates that the best F_1 hybrids are generally superior to synthetic varieties. Selfing and the production of F_1 hybrids have been powerful tools for improvement of cross-fertilizing crops; with the possibilities of diploidization of haploids and cytoplasmic male sterility, they can be equally valuable for improvement of forest trees.

Increased population buffering to enhance fitness of mass-produced, rust-resistant hybrid or synthetic varieties of forest trees could be obtained through seed blends. Mass production of "multilineal seed blends" will depend on practical methods for the production of hybrid lines. The development of such blends resistant to different races of the rusts will not be possible until rust races have been identified; and new races of the rusts would not be expected to develop until there are extensive plantations of a rust-resistant variety.

Clonal and seedling seed orchards are the base populations--the Syn-0 generations--for the production of synthetic varieties that are propagated by seed. The open-pollinated progenies of clonal orchards after roguing that has been based on progeny tests will be Syn-1 synthetics; the open-pollinated progenies for seedling seed orchards after phenotypic roguing will be "mass-selection" synthetics. Seed-increase to produce Syn-2 foundation seed and Syn-3 certified or registered seed (as in agricultural crops) is neither practical nor anticipated for forest trees; seed orchards are generally large enough to meet the forestation requirements of the organizations that establish them. Genetically improved synthetic varieties will require parental populations with high general combining ability, not only for special traits, but also for a high degree of fitness.

Multiclonal hybrid varieties would be mixtures of clones (intra- or interspecific hybrids, or both) selected for a high degree of vegetative fitness and for special traits, such as growth rate, timber form, and resistance to pests. The genetic gain will depend upon the *average*

performance of genetically superior individuals, not on the average performance of families or lines. Such exceptionally superior *individuals* may be obtained in early generations of intensive breeding, or even by intensive selection in progenies derived from gene pools or natural populations. Clonal tests of rust-free *Pinus strobus* ortets selected in natural stands have demonstrated a broad range of inherent, individual susceptibility; from high resistance (if not immunity) to extreme susceptibility. The clones in a multiclonal variety could be changed on very short notice, because the breeder could multiply superior genotypes for commercial use *without adulteration of the genotype and without determining their combining ability to transmit the desirable qualities or characteristics.*

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FLOOR DISCUSSION

ZUFA: Dr. Borlaug, did you say that a newly produced rust resistant multilineal wheat variety could be used for only 5 to 15 years?

BORLAUG: For conventional varieties, the average life in winter climates is 15 years. When you move them into the tropics where the rust persists the year around, it's likely to be 5 or 6 years.

ZUFA: Dr. Schreiner, how would that apply to our blister rust resistant white pine varieties?

SCHREINER: The answer to that question will have to wait until we plant some improved varieties and find out how fast the fungus mutates.

CAMPANA: There is some recent evidence of air pollution damage to eastern white pine (*P. strobus*) in the East (i.e., U.S.A.). Would you care to speculate on the breeding situation in view of this new evidence?

SCHREINER: Yes, I'm glad you asked that, because this may raise the time required for creation of pest-resistant *seed varieties*, including resistance to air pollution, to well over 100 years. But I predict that we can get such resistance. We have observational evidence that we have

resistant individuals in the Northeast, and the U. S. Forest Service Southeastern Forest Experiment Station has some very resistant types. If you consider the possibilities of selfing through the diploidization of haploids in order to shorten the inbreeding and back-crossing cycles, it may not take too many years; early flowering, if we can use it, may help. We need only about 50 or 60 individuals for multiclonal varieties. I think we can incorporate air pollution resistance. Our air pollution in the Northeast is not critical with respect to forest production. We would not, at present, need such resistance if we had weevil resistance, which is essential.

WEISSENBERGER: Dr. Schreiner, you mentioned the use of diploidization of haploids. Do you think that would substitute for inbred lines, or would you like to use it for specific combining ability?

SCHREINER: I am assuming we could use it for inbred lines in one step. I have discussed this with Dr. Gustaffson (Swedish Royal College of Forestry); he also believes that this is a possibility. I think Chase, in his work with corn, was the first to use this procedure.

BORLAUG: This has, I think, very interesting possibilities. It is something that should be looked at. Not only looked at, somebody needs to sweat at it.

DUFFIELD: I'm not sure which way this question is aimed, but I would like to suggest that the poplars would seem to be suited to the approach that Ernie is advocating. And, I have a question--why are northern Italy and Yugoslavia still planting larger stands of I-214. There must be some practical reason for doing it.

SCHREINER: I suspect you want me to say that there is a poplar clone, I-214, that really has a very broad built-in buffering system. This is probably true, but we must remember the stands are cut at 12 to 14 years; the rotation is usually less than 15 years. I have seen very few older plantations. But, Jack, I think that time is beginning to run out, even on this excellent clone. *Marssonina* may be increasing on this clone. I suspect that the rapid, recent increase of *Marssonina* on poplar clones in Europe is due, at least in part, to the extensive monoclonal cultures.

BORLAUG: I'd like to make one comment. I think that one of the "other additional chores or jobs" that a scientist has to do is to promote research. Ernie Schreiner has had I don't know how many years at tree breeding and he's still the apostle. He can promote, and we hope that he will continue to do this for forest genetics and forest tree breeding, because without this, there can be no increase in the funds that are so badly needed in order to keep these long-range programs going. This kind of spirit and this kind of attitude, I hope, will inspire young people to follow the lead that he has given us during these past 30 years. His enthusiasm has provoked people to do their best.

SCHREINER: Forty-four years.

BORLAUG: Forty-four? I didn't know quite how long it was, but I remember back in 1935 when I worked out at the Hopkins Experimental Forest in Williamstown, Massachusetts, shortly before Ernie moved in, that he had been at it for quite a while then.

MULTIPLE TRAIT SELECTION IN WHITE PINE BREEDING SYSTEMS: BLISTER RUST RESISTANCE, WEEVIL RESISTANCE, TIMBER YIELD[1]

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ABSTRACT

A white pine variety with improved resistance to both white pine blister rust and white pine weevil would be useful in certain regions of North America. Some form of multiple trait selection in a fairly complex breeding system would be required to produce it. Forest and nursery environments are used as examples in discussing the efficiency of selection and possibilities of bias due to interference between methods of evaluating growth, rust incidence, and weevil damage. The advantages of using index selection rather than independent culling levels or tandem selection are considered, as well as some potential disadvantages. Interactions of the two pests on their common host in different environments are likely to introduce bias into estimates of means and genetic variances. Mortality caused by rust and weevils may be another source of bias, and may also restrict opportunities for index selection. In order to reduce complexity and to maximize genetic progress without excessive risks, separate selection and testing for resistance to the two pests is suggested at first. Initial goals would be to find two sets of parents each having superior breeding values for resistance to one of the pests, and to estimate parameters for two separate selection indices. Ultimately a single selection index may be developed which includes blister rust resistance, weevil resistance, and other traits related to economic timber yield.

INTRODUCTION

Numerous white pine breeding programs in North America focus on genetic improvement in *Pinus strobus* L., *P. monticola* Dougl., and *P. lambertiana* Dougl. Most of the programs have existed less than 10 years, and few of them for as long as 20 years. Their improvement objectives, being related to different environmental and economic conditions, vary in several respects. In some regions the damage caused by white pine

[1] *Research on white pine weevil resistance has been supported by Forest Service, USDA, Grant #1 and by Northeast Regional Research Project NE 27, USDA. Authorized on July 28, 1969, as Paper No. 3634 in the Journal Series of the Pennsylvania Agricultural Experiment Station.*

blister rust (*Cronartium ribicola* J. C. Fisch. ex Rabenh.) or by white pine weevil (*Pissodes strobi* Peck) is so severe that improved resistance to one or the other pathogen obviously deserves primary emphasis. Elsewhere these pathogens cause little or no damage, so that timber yield may be improved more directly through traits such as growth rate, adaptation to climatic factors, or wood quality. Although the ultimate objective of a program may be to improve the economic yield of timber, a single trait, in practice this is commonly pursued by selection for multiple traits that are known or assumed to be closely correlated with yield.

If disease resistance is one of the important objectives in a tree breeding program, rather severe restrictions may be placed on the selection method. Certain selection systems for resistance to white pine blister rust (Bingham *et al.*, 1969; Patton and Riker, 1966) and to white pine weevil (Soles, Gerhold, and Palpant, 1969) obtain genetic information and discard large proportions of populations at early ages and in atypical environments. Resistance to both of these pathogens would be useful in parts of Wisconsin, Michigan, Ontario, New York, and New England. Consequently, it may be useful to question whether selection for both types of resistance, together with other traits determining yield, would be compatible.

So that we may have some concrete examples in mind, let us consider two hypothetical selection schemes as outlined in Table 1. Both employ progeny testing to evaluate genetic variances of resistance to white pine blister rust, of resistance to white pine weevil, and of other traits related to yield. The term "growth" is used loosely to refer to yield-related traits such as height, diameter, and wood quality. In Scheme 1 all traits are evaluated in forest plantings; in Scheme 2 the two types of resistance are evaluated under artificial conditions in a nursery and growth is measured later in forest plantings. In the nursery, seedlings under shelters are inoculated with rust spores in August at age 2 and/or 3, then exposed to weevils in cages during May at ages 3 and 4. About 15% of the original population may survive for outplanting at age 5. The percent of healthy and unweeviled survivors may approach 0 at age 20 in Scheme 1 and at age 15 in Scheme 2. A high selection intensity for resistance may therefore be achieved in both schemes before there is sufficient flowering to proceed to the next generation. Parents with superior resistance breeding values may be identified by age 4 in Scheme 2, however, while about 12 to 15 years would be required in Scheme 1. The degree of contrast between the two models obviously could be altered without foresaking biological realities.

PROBLEMS RAISED BY MULTIPLE TRAIT SELECTION

The selection schemes that we are contemplating are rather complex. Many problems would be encountered in judging their utility and in developing detailed procedures for them. It will be possible to consider just a few of the major problems here, and to make only a start in seeking solutions. The matters that will concern us are the efficiency of selection, and the possible interference between evaluation methods for rust, weevil, and growth, which might introduce bias.

The traits under selection and the genetic parameters of interest are listed in Table 2. Growth rate, blister rust resistance, and weevil resistance are viewed as component traits, each correlated with the complex trait, yield. Selection for any one or several of the correlated

Table 1. Two hypothetical schemes for evaluating resistance to white pine blister rust and to white pine weevil in a breeding program, indicating procedures and percentages of healthy and unweeviled survivors at various ages

	Scheme 1, Forest exposure			Scheme 2, Nursery and forest exposure		
	Survivors after attack by:			Survivors after attack by:		
Age	Rust	Weevil	Either	Rust	Weevil	Either
2-3		outplant		expose		
3-4	100	100	100		expose	
4				30	50	15
				evaluate resistance		
5	95	98	93		outplant	15
10	60	45	27	8	7	0.56
15	20	5	1	3	2	0.06
20	4	2	0.08			
?		evaluate resistance and growth			evaluate growth	

Table 2. Genetic parameters of traits correlated with yield of white pine

Phenotypes	Phenotypic correlations	Additive genetic values	Genetic correlations	Heritabilities
G, growth rate	R_{GY}	g	r_{gy}	h_g
	R_{BG}		r_{bg}	
B, blister rust resistance	R_{BY}	b	r_{by}	h_b
	R_{BW}		r_{bw}	
W, weevil resistance	R_{WY}	w	r_{wy}	h_w
Y, yield	R_{GW}	y	r_{gw}	h_y

traits would in effect be indirect selection for yield. Falconer (1960) and Searle (1965) have outlined conditions under which indirect selection may be more advantageous than direct selection, and Scheinberg (1967) has developed a method for computing the sampling variance of relative efficiency estimates using variance-covariance components from sibship data.

There are some obvious opportunities for achieving more rapid progress in white pine breeding by using indirect selection. For example, if height growth to age 20 gives a good estimate of yield at maturity, age 80, and if h_g were not greatly inferior to h_y/r_{gy}^2, the genetic rate of gain per unit of time would be multiplied several fold. Furthermore, if blister rust is the major determinant of yield in areas where the risk of infection is high, and if h_b measured under uniform rust nursery conditions is much larger than h_y measured in a highly variable forest environment, the efficiency of improving yield may be increased by selecting for blister rust resistance instead of, or in addition to, measuring height growth or yield itself. A similar proposition could be stated for weevil resistance. In such cases the assumption that resistance genes found in a nursery will be useful in forest plantings needs to be confirmed.

If faster growth rate, blister rust resistance, and weevil resistance are all valid selection objectives, how may selection best be applied to give maximum improvement of economic yield? Lerner (1958, p. 176) and Falconer (1960, p. 324) have given theoretical and experimental information about selection for more than one trait. *Tandem* selection, in which one trait is selected for after another, and *independent culling levels*, in which individuals are rejected if they fail to meet any of the minimum standards set for each trait, are considered to be less effective than *index* selection, which is based on a total score combining genetic and economic values of all traits. For three traits, the relative selection efficiencies are 1.0 for tandem, 1.7 for independent culling levels, and 2.0 for index selection, according to Lerner (1958), who made the comparison under several simplifying assumptions. Falconer (1960) points out that the advantages of an index are less if family selection is practiced, and suggests that little efficiency will be lost if each phenotypic value in this situation is weighted only by its relative economic importance.

Multiple trait selection also has several potential disadvantages or pitfalls of which breeders should be aware. Even though total economic gain is expected to be superior, the gain for each component trait will not be as great because its selection intensity will be lower. To illustrate, if the best 1% of the individuals in a larger population are selected for each of two uncorrelated traits, the effective selection differential for each will be 1.75 σ instead of 2.67 σ. The effectiveness also can be lowered by negative genetic correlations, and if these are pleiotropically determined it may not even be feasible to reach an improvement goal involving two traits. There is a tendency for white pine weevils to attack the taller trees, and this might (or might not) cause r_{wg} to be negative. Genetic correlations may change in different environments or in successive generations as a result of selection pressure. This complicates the design of progeny tests. The assigning of economic weights can also be troublesome, especially in view of the long-time span over which the values of timber crops must be predicted and because changing disease and insect control measures must be anticipated. These few examples illustrate the complexity of constructing

a selection index and the need for making appropriate estimates of its parameters. Selection in tandem or by culling levels may be practiced much more simply, but if important genetic correlations or economic values are consequently overlooked, a breeder may risk being deluded about his actual genetic progress.

Proceeding on the premise that multiple trait selection may be theoretically superior under some conditions, let us examine next whether it may be put into practice without interference between the methods of estimating the genetic parameters. The fact that two pathogens would be interacting with their common host is cause for concern that expressions of resistance to blister rust may be altered by concurrent weevil attack, or vice versa. It would be important to determine for *individuals* the magnitude and duration of such an effect, if it exists. Its effective magnitude on a *population* would be smaller in Scheme 1, because the probability of simultaneous infection would be lower unless it were purposely prevented in Scheme 2. The greater control over artificial exposure in Scheme 2 may provide a means of avoiding an interaction of pathogens entirely, if the duration of the effect were brief enough. Either blister rust or weevil attack certainly would reduce height growth, and furthermore it is easy to imagine that any of these relationships could interact with variable environments. It is therefore very likely that interactions would be a source of bias, and it must be decided whether to measure them or to avoid them.

Other problems arise from the fact that, before growth is measured, most original members of populations will be lost, either gradually in Scheme 1 or quite suddenly in Scheme 2. Blister rust would be the cause of 96% mortality in Scheme 1, compared to 82% in Scheme 2 plus 15% mortality due to weevils. Although it is desirable to have fairly high levels of infection in order to secure high selection intensities, the measurements of growth could be seriously biased if R_{BG} or R_{GW} were large. A second consequence is that a large amount of tandem selection already would have been imposed by the pathogens, thus greatly restricting subsequent opportunities for index selection.

A white pine breeder setting out to improve both rust and weevil resistance is faced with more technical questions than he can resolve all at once. We have explored the impact of some of the problems, but have not even considered such important matters as mating designs, methods of mass-producing improved varieties, and possible changes in pathogenicity. Therefore, it appears that some means of simplifying this complex situation must be found.

STRATEGY FOR SEEKING SOLUTIONS

How can the breeder best take advantage of opportunities for maximizing genetic progress without raising risks of serious mistakes to unacceptable levels? With so many uncertainties facing him, should he postpone all improvement efforts until research has provided complete information upon which to base his decisions? Or should he plunge ahead to select and propagate the phenotypes that please him, ignoring the hazards that he should confront and assuming with blind confidence that his personal judgement can be substituted for facts?

Clearly, the best answer will be found somewhere between these two extremes. Predicted and actual genetic gains will depend on valid genetic information. Yet the data must be derived from the parent genotypes which should be selected on the basis of this same information. This dilemma exists in every dynamic breeding scheme because the parents and genetic parameters change in subsequent generations. The breeder aims for the ideal solution through a series of approximations, using a judicious mixture of hard facts, experienced judgment, and faith. Resources must be committed at the outset both to finding superior genotypes and to obtaining genetic information. Neither element can be sacrificed completely, but the relative amount of effort devoted to each may be shifted toward the greater need.

In my opinion the greater need in the situation that we have been examining is for better definition of genetic parameters involving the two pathogens. My recommendation is to resolve the difficulties in two steps by dividing the ultimate improvement goal into two intermediate goals. In other words, genes that confer resistance to blister rust would be selected separately from those that confer resistance to white pine weevil, thereby reserving the more complex interactions for later generations. Accordingly, the following suggestions are offered for the first generation:

1. Choose two sets of parents, one for blister rust resistance and the other for weevil resistance. Maximize selection intensity for resistance in each, merely avoiding negative selection for other yield-related traits.

2. Restrict matings to within each set of parents.

3. Test resistance in two sets of environments, protecting each set against the other pathogen. Test each set of parents for resistance only against the pathogen considered in its selection.

4. Subdivide each family for testing, exposing a larger portion to the pathogen in the nursery, and comparing survivors with the unexposed portion in forest plantings to determine the validity of nursery selections. Take measurements at about 4-year intervals to define growth and mortality trends and their interrelations.

5. Obtain the data needed for two independent selection indices, each containing parameters of growth and of resistance to one or the other pathogen. Compared to simpler selection methods, index selection offers greater efficiency and discipline in accounting for genetic and economic factors that influence genetic gains and their values.

During the first generation a firm foundation would be laid for further progress, possibly sacrificing some genetic gain in favor of lower risk and greater flexibility. A decision on combining both types of resistance into a single variety would be postponed until some of the uncertainties have been clarified. In the meantime two improved varieties, each with one type of resistance, could be produced and could be used silviculturally, singly or in mixture, in conjunction with other measures for controlling blister rust or weevils.

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FLOOR DISCUSSION

Panel leader Borlaug withheld discussion of this paper until after Dr. Steenackers' paper, immediately following.

BREEDING POPLARS RESISTANT TO VARIOUS DISEASES

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ABSTRACT

Poplar culture in Europe is threatened by several diseases, especially since it is based mostly on a small number of *Populus euramericana* (the hybrid of *P. deltoides* x *P. nigra*) clones. Securing multiple resistance to diseases of the locality is a necessary first step in any long-term poplar breeding program.

Activities of the author's Institute in testing resistance of thousands of new clones of 4 *Populus* spp. to diseases caused by *Taphrina aurea, Marssonina brunnea, M. populi, Melampsora* spp., *Septoria populi, Septotinia populipoeda, Dothichiza populea* and *Aplanobacterium populi*, plus a virus, are reviewed. For each poplar:disease combination highly resistant (even immune) clones have been selected. Certain *P. deltoides* clones have been selected as resistant to the above disease organisms except *A. populi*; however, a few of these clones are even resistant to this bacterial canker. *P. nigra* clones are generally resistant to bacterial canker, but not to *D. populea*. Clones of *P. trichocarpa* resistant to bacteria canker are opening up new possibilities for utilizing this poplar.

Clones demonstrating multiple resistance are transplanted to plantations, which after 8-10 years become seed orchards and breeding arboreta. Orchard clones are used in a continuing program of greenhouse, full-sib matings. F_1 and F_2 families or clones with sufficiently high multiple resistance have been obtained from crossings of *P. deltoides* x *P. trichocarpa* crosses. Studies on the heritability of resistance to the various poplar diseases are underway.

INTRODUCTION

Although many diseases can affect poplar species and their hybrids, poplar cultivation in Europe has for years been based on a very few *Populus euramericana* (Dode) Guinier (the hybrid of *P. deltoides* Bartr. x *P. nigra* L. clones. Consequently, poplar cultivation is permanently threatened by diseases.

A long-term poplar breeding program must concentrate on breeding new poplars with increasing resistance to different diseases. The pure species are, without doubt, the best basic material for such a breeding program. Furthermore, interspecific crosses are as important as intraspecific crosses in breeding poplar clones with the necessary multiple resistance to these diseases.

THE POPLAR SPECIES USED IN OUR BREEDING WORK

For the past 15 years our Institute has concentrated its breeding work on the native species *P. nigra* and the three imported species *P. deltoides*, *P. trichocarpa* Torrey and Gray, and *P. maximowiczii* Henry. Our collections of these species are increasing every year. New provenances of seedlings and cuttings received from abroad or produced at the institute are being added.

Our yearly production of seedlings, offspring of full-sib, intra- and interspecific crossings in greenhouses, varies between 10 and 15 thousand seedlings. Our experimental plantations of the species now produce an inexhaustible quantity of half-sib progenies.

TESTING NEW POPLAR CLONES FOR RESISTANCE TO VARIOUS DISEASES

New clones are cultivated in nursery and experimental plots for several years. Here the plants and young trees are exposed to *natural infection* by several disease organisms, of which the more important ones are listed below:

Taphrina aurea Pers. ex Fr. (leaf blister)
Marssonina brunnea (Ell. & Ev.) Magn. (leaf blight)
Marssonina populi (Lib.) Hagn. (leaf blight)
Melampsora spp. (leaf rusts)
Septoria populi Desm. (leaf spot)
Septotinia populiperda Waterman & Cash (leafblotch)
Dothichiza populea Sacc. & Briard (bark necrosis)
Aplanobacterium populi Ridé (bacterial canker)
Virus

Normally, most of these diseases affect the poplars at an early stage (1, 2, and 3 years of age).

Elimination of the seedlings that are very susceptible to leaf rust has already started by the end of the first year, and is continued in the following years.

The reaction of each clone to a particular disease is evaluated on the basis of frequent field observations or, in the case of bacterial canker, on the basis of the reaction after artificial inoculation.

Bacterial canker (*A. populi*) normally affects young poplar trees in nature only at an age of 8 to 10 years. Therefore, the reaction of the different clones of our collection to this dangerous disease is tested by artificial inoculation tests on 1- to 3-year-old shoots. This test is efficient. In collaboration with Mr. Ridé (France), 5,000 to 10,000 young shoots per year can be artificially inoculated with strains of *A. populi*.

After several years of repeated observations each clone will receive a score of 0 to 5 for each disease. The score 0 is attributed to a clone which seems to be completely immune to the disease and 5 signifies maximum susceptibility. Growth of the clones is not affected when the disease score is from 0 to 2. For breeding purposes, however, it is important and even necessary to use only the clones with the highest resistance (score 0 or 1).

RESULTS OBTAINED BY SELECTION IN NATURAL POPULATIONS

During the last 15 years we have examined the reaction of thousands of clones of *P. nigra*, *P. deltoides*, *P. trichocarpa* and *P. maximowiczii*. Table 1 summarizes the results of these observations. The scores in Table 1 are only valuable for the clones of the four species that are presently in our collections. There are always different points which are at the moment not quite clear, for example, the reaction of *P. nigra* and *P. trichocarpa* to virus is not well known. Also, a number of observations have been made for *S. populi* and *S. populiperda*. We hope to complete the scoring on these in future years.

Within each species and for each disease a number of clones have been selected which are highly resistant or even immune. However, there are no clones of *P. nigra* and *P. trichocarpa* which are completely free of leaf rusts. The clones of *P. nigra* are all susceptible to *D. populea*, as well. Moreover, most of the clones which are highly resistant or immune to one disease are not useful in a poplar plantation because of their susceptibility to one or more other diseases.

POPULUS DELTOIDES

Clones of *P. deltoides* have been selected that are, at the same time, immune or highly resistant to *T. aurea*, *Marssonina* spp., *Melampsora* spp., *S. populi*, *S. populiperda* and *D. populea*. However, about 90% of these clones are too susceptible to bacterial canker (*A. populi*) to be used in a general manner. But, most of these clones are very useful in Europe, south of about 47° N latitude, where bacterial canker is usually absent.

During the last few years we succeeded in selecting a few clones of *P. deltoides* that are highly resistant to all the above diseases including *A. populi*. These *P. deltoides* clones are useful in breeding work at all latitudes.

POPULUS NIGRA

Because of their general susceptibility to rust and *D. populea*, the clones of *P. nigra* are not useful in the commercial poplar plantations of western Europe. On the other hand, these clones are extremely resistant to bacterial canker and therefore are valuable in intraspecific crosses with *P. deltoides*.

Table 1. The reaction of clones of four poplar species to various poplar diseases in western Europe

Disease organism	Clones of poplar species			
	P. maximowiczii	*P. trichocarpa*	*P. nigra*	*P. deltoides*
	disease score[a]			
Taphrina aurea	0 1 2 - - -	0 1 2 - - -	0 1 2 3 4 -	0 1 2 - - -
Marssonina brunnea	0 1 - - - -	0 1 - - - -	0 1 2 - - -	0 1 2 3 4 5
Marssonina populi	?	0 ? - - - -	0 1 2 3 4 5	0 1? - - - -
Melampsora spp.	- - 2 3 4 -	- - 2 3 4 5	- - 2 3 4 5	0 1 2 3 4 5
Virus	?	?	0 1? - - - -	0 1 2 3 4 5
Dothichiza populea	0 - - - - -	0 1 2 - - -	- - 2 3 4 5	0 1 2 - - -
Aplanobacterium populi	- - 2 3 4 5	0 1 2 3 4 5	0 1? - - - -	0 1 2 3 4 5

[a] Disease scores: 0 = immune, 5 = highly susceptible

POPULUS TRICHOCARPA

The possibilities of using *P. trichocarpa* in poplar plantations are increasing since, with the help of the "Ridé test", we succeeded in selecting several clones that are highly resistant to bacterial canker. The same clones are also highly resistant to *D. populea*.

POPULUS MAXIMOWICZII

The clones of *P. maximowiczii* are somewhat susceptible to rust and bacterial canker, and therefore not directly useful in our plantations. However, we obtained interesting results from the interspecific crosses with *P. deltoides* and *P. trichocarpa*.

RESULTS OBTAINED WITH HALF-SIB CROSSINGS

By simple selection in natural populations we succeeded in isolating several clones of *P. deltoides* and *P. trichocarpa* that seem to have sufficient multiple resistance to the most important western European diseases. These clones will be used in our commercial poplar plantations.

At about 10 years of age, each of these plantations will be a possible seed orchard. Here seed collections of half-sib and even full-sib crosses may be collected at an extremely low cost.

During summer 1969 we obtained about 3,500 seedlings for each of 75 different half-sib offsprings of selected *P. deltoides* parent trees. It certainly seems possible that we can select, from these seedlings, a number of clones with increasing multiple resistance to the various diseases.

There are similar possibilities within the species *P. nigra* and *P. maximowiczii*. But since it is nearly impossible to establish in Europe, economically valuable plantations with these two species, the breeder will have to pay the total cost of experimental plantations and seed orchards.

RESULTS OBTAINED WITH FULL-SIB CROSSINGS

For several years we have made many different intra- and interspecific crosses between clones of *P. nigra*, *P. deltoides*, *P. trichocarpa* and *P. maximowiczii* that show high multiple resistance (Table 1). The seedlings of these crosses are subjected to the diseases listed in Table 1 through field tests except for bacterial canker. Later on, the best of these seedlings are inoculated with bacterial canker.

Populus deltoides x *Populus deltoides*

Several F_1 and F_2 crosses have already been made between different *P. deltoides* clones which are immune or highly resistant to all the diseases listed in Table 1 except for bacterial canker. Multiple resistance has remarkably increased for most of the second generation crosses.

This means that the seedling plantations established with these poplars at a latitude of 45° N, in an area free of bacterial canker, are

healthy and growing good. Besides the clonal selection, these plantations may give us, in the near future, seedlings of selected *P. deltoides* crosses for commercial plantations.

Populus trichocarpa x *Populus trichocarpa*

Several crosses have been made between parent clones which are highly resistant to bacterial canker and to *D. populea*. The results also indicate that there is a good possibility of reducing the susceptibility to rust of *P. trichocarpa* due to transgressive variation in subsequent generations. In the meantime the selected clones may be used in commercial plantations to produce wood and seeds.

These same selected *P. trichocarpa* clones are used in interspecific crosses with *P. deltoides* and *P. maximowiczii*.

Populus nigra x *Populus nigra*

Numerous intraspecific crosses have been made that produce clones which are less susceptible to rust and *D. populea* but that remain resistant to bacterial canker. There already appears to be a possibility of selecting less rust-susceptible clones in the F_2 generation.

Populus nigra in general is very useful in producing *P. deltoides* x *P. nigra* hybrids which are resistant to bacterial canker.

Populus maximowiczii x *Populus maximowiczii*

All of our *P. maximowiczii* clones are highly susceptible to bacterial canker. Therefore we have made only a few intraspecific crosses.

INTERSPECIFIC HYBRIDS

We have selected several useful interspecific hybrid clones from the following F_1 crosses:

P. deltoides x *P. nigra*
P. deltoides x *P. trichocarpa*
P. deltoides x *P. maximowiczii*
P. trichocarpa x *P. maximowiczii*

Where the old European hybrid clones have disease scores varying from 2 to 5 the new hybrid clones have a much higher multiple resistance. Their scores vary between 0 and 3.

It is again important to emphasize that the choice of the parent trees and of the interspecific crosses depends upon the clonal reaction of each species to the various diseases.

In general, however, we can say that resistance to most of the leaf diseases is transmitted by *P. deltoides*. The resistance to *D. populea* is inherited from *P. deltoides* or *P. trichocarpa* or *P. maximowiczii*. Bacterial canker resistance is introduced from the bacterial canker resistant *P. deltoides*, *P. nigra*, or *P. trichocarpa*.

Recently, we have completed the second generation (F_2) crosses and backcrosses using some of the best of the new clones. Several

experimental plantations are already established with the best F_1 hybrid clones.

Clones of *P. nigra*, *P. deltoides*, *P. trichocarpa*, and *P. maximowiczii* can be selected that are resistant to one or more of the diseases. These selections must be continued, since the basic collection of resistant parent clones will never be very large in a long-term breeding program.

CONCLUSIONS

Close cooperation of plant pathologists and plant breeders will more and more enlarge our knowledge on the resistance of poplar clones to various diseases. A striking example of such collaboration is the number of new bacterial canker-resistant poplar varieties that are added yearly under the supervision of Ridé and tested in our nursery.

Individual resistance in parent clones to the various diseases can be transmitted to the offspring. Moreover, resistance to several diseases can be combined in one full-sib offspring and even in one clone.

Studies have already been started to gather more information on the heritability of resistance to the various diseases and on the kind and number of genes involved.

FLOOR DISCUSSION

(Also covering the preceding paper by Henry D. Gerhold.)

KRIEBEL: I have a few comments regarding Dr. Gerhold's paper on the multiple selection for weevil resistance, rust resistance, and growth of white pine. This is a real problem and I think from a theoretical standpoint I would agree that it would be necessary to select independently, but I see some practical problems. Our programs are based on certain long-range utilization objectives, and some things may disrupt these objectives. For instance, it's conceivable that 50 years from now, we won't care whether a white pine tree is straight or not. It's conceivable that the main use of white pine might be fiber, and we might be using huge combine-type harvesting machines that move through the woods grinding up everything as they go along, so that a weeviled tree wouldn't be a disadvantage as compared to a straight tree. In fact, such machines are already under development. However, in my program, I am certainly assuming that there is going to be a continuation of demand for straight white pines. Operating on that basis there is a problem in selecting simultaneously for even two of these traits, not to mention three. There are some other considerations. One is that we do have at least one exotic species of white pine (*Pinus peuce*), which appears to have resistance to both weevil and blister rust. It offers good selection possibilites and opportunities for hybridization. It would be necessary to select for combining ability with respect to seed yield of individual parents, but I think there is a good possibility to simultaneously select hybrids of *P. strobus* x *P. peuce* for both weevil resistance and blister rust resistance. The problem is that these hybrids are not as vigorous as some of

the other white pine hybrids, but the vigor is not too bad. Also, multiple trait selection may be feasible. It would be impossible to combine selection for growth and weevil resistance at the same time once the trees were weeviled, because it is very difficult to assess height growth of weeviled trees. But we can select for different traits at different ages in the same tree, assuming that it's possible to evaluate height growth at an early age. Perhaps the trees could be sprayed for a few years to protect them from the weevil; during this period, one could assess height growth, then stop spraying and test for weevil resistance. This would have to be done on a very uniform site to avoid environmental variations which would reduce the effectiveness of selection for height growth, but it could be done on a small area, especially if caging techniques were used. These are a few ideas I'd like to throw out for consideration.

HEIMBURGER: I believe that it would be possible to do both except that frequency of blister rust resistance in *P. strobus* is very low. It's about one in 10,000 to one in 1,000, and therefore, you have to start with very large numbers, and the same thing with weevil resistance. It depends very much on the provenance. Some provenances are much more weevil resistant than others. All the materials from eastern North America near the Atlantic are much more weeviled than the western provenances of *P. strobus*. There leader thickness is a very important factor which can be very simply measured in the nursery stage, and there is a good correlation between leader thickness of adult trees and leader thickness of seedlings. We have one provenance where we collected seeds from a tree, and we measured the leader thickness of the seedlings and they were all much thinner in this population. So, I would stick to scheme two of Gerhold but would add to it that we need plenty more. That the frequency of resistance is low for blister rust and quite variable in relation to weevil, depending on the provenance.

BECKER: I am delighted to hear Dr. Gerhold discuss some animal breeding systems called tandem index selection and culling levels. I have been listening to various people discuss breeding systems, and it appeared to me you have been using the cereal crop systems as your model, and yet in working here in Moscow, I have always had the feeling that tree breeding was much closer to animals than it was to the cereal crops. I know this may shock you a bit, but I consider trees out in the Far East as being bull No. 1. Now, I'd like to comment on these three systems that you have proposed. I would say that the tandem method would be almost an impossibility. You have too long a generation time to do this. Tandem method means you would select for growth for say five generations, then you would shift to selecting for blister rust resistance for five generations, then you would shift to weevil resistance for five generations. Well, this seems to be much too long, and actually, in animal breeding, there is very little of this going on. This was just a suggestion thrown out by Hazel way back in the early days. Never really practiced by animal breeders. The next one would be index selection, and I believe this might be possible if you had full-sibs in three different areas where you more or less simultaneously subjected one group to blister rust exposure and another group to weevil exposure, and another group that you measured for growth. Then you put it into a grand index and it comes out in a computer that says select such and such a family. However, this does seem to have some problems too. I don't think you're going to do that, really, from my slight experience with forest tree breeding. So this leaves the other method, which really you have outlined

in your Table 1 which is individual culling level. Now, it seems to me that you still could follow this approach of having three different replications of the same full-sib family, one of which you expose at say age 2 or 3. I leave that to the foresters. But somewhere along the line you have to expose them. Then, in another group you expose the families to the weevils at whatever age it is most tender. Then one can pick out the various ones and mate them together. I am not sure if full-sib mating will work out too well, but it does seem to me your individual culling levels are the best scheme I have heard here. I'd have to look at some data. I don't believe you have too much of this, do you?

GERHOLD: No, not pertaining to weevil resistance.

BECKER: We are trying to generate some for blister rust resistance which you heard yesterday. It's not very easy.

KRIEBEL: If you have extremely low frequencies of blister rust resistant trees, 1 in 10,000 has been suggested and if the level of weevil resistance was also 1 in 10,000, the number of individuals containing both traits would be 1 in a hundred million. And when growth is added, your chances of finding a tree that combined all of these traits is infinitely small.

A WHITE PINE BLISTER RUST RESISTANCE BREEDING PROJECT IN NORTHEASTERN MINNESOTA[1]

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ABSTRACT

The breeding project here briefly described has been designed primarily for a low budget. The design also makes it feasible to utilize a broad genetic base of selections in the initial phase of the program.

Phase I consists of the phenotypic (mass) selection of ca. 1,000 *Pinus strobus* mother-trees in the high white pine blister rust (*Cronartium ribicola*) infection areas of northeastern Minnesota. About 100 plants grown from open-pollinated seed of each of these selections (i.e., ca. 100,000 plants) are being propagated and outplanted on a high infection site near Tofte, Minnesota, and subjected to a natural screening for rust resistance.

The surviving plants will be allowed to inter-pollinate and the seed may be used for commercial outplantings. Genetic gain in resistance may be expected to be rather low at this stage, possibly in the order of 12 to 15 percent.

Flowering by the age of 15 to 20 years in the surviving plants of the screen test will permit initiation of the final recurrent family selection phases of the improvement program. Total genetic gains in such full-sib family selection may hopefully be expected to range from 30 to 40 percent in the first generation and possibly higher in succeeding generations.

In spite of a lengthened time schedule, the advantages of this mass selection-screen test phase are: (1) The large number of trees screened will provide a broad genetic base for later improvement of rust resistance and other desirable characteristics, (2) the uniformity of treatment in the screen test makes the possibility of "escapes" lower than in nature, (3) costs of breeding with these trees will be low because of uniform age, size, and proximity in which they will be growing, and (4) the planting design can be adapted to tests of various techniques such as fertilizers to hasten flowering.

[1]*A cooperative project involving the U. S. Forest Service, Quetico-Superior Wilderness Research Center, and the School of Forestry, University of Minnesota.*

[2]*Editor's note: Dr. Pauley's distinguished career in forest genetics ended with his death in April 1970.*

INTRODUCTION AND SUMMARY

The breeding project here briefly described has been designed primarily for a low budget. The design also makes it feasible to utilize a broad genetic base of selections in the first phase of the program.

The initial phase consists of the phenotypic (mass) selection of about 1,000 *Pinus strobus* L. mother-trees in the high rust infection areas of northeastern Minnesota. About 100 plants grown from open-pollinated seed of each of these selections (i.e., ca. 100,000 plants) are being propagated and outplanted on a high infection site near Tofte, Minnesota, and subjected to a natural screening for rust resistance.

The surviving plants will be allowed to inter-pollinate and the seed may be used for commercial outplantings. Genetic gain in resistance may be expected to be rather low at this stage, possibly in the order of 12 to 15 percent.

Flowering by the age of 15 to 20 years in the surviving plants of the screen test will permit initiation of the final recurrent family selection phases of the improvement program. Total genetic gains in such full-sib family selection may hopefully be expected to range from 30 to 40 percent in the first generation and possibly higher in succeeding generations.

In spite of a necessarily lengthened time schedule the advantages of the proposed initial mass selection-screen test phase may be summarized as follows:

1. The genetic base would be much broader because of the large number of trees initially screened. This involves improvement considerations other than rust resistance since, in the family selection phases of the program, traits such as growth rate, branching characteristics, weevil resistance, etc., may logically be incorporated. With such a broad genetic base, isolation of rust-resistant lines combined with other desirable traits would be easier than in a population initially restricted in size.

2. Due to uniformity of treatment in the screen test the possibility of highly susceptible "escapes" would probably be much lower than in wild trees growing in widely diverse habitats.

3. The fact that the surviving trees in the screen test will be of the same age, uniform in size when sexual maturity is reached, and close together will greatly reduce controlled pollination costs, especially labor for bagging, travel, etc.

4. Uniform age of the stock and design of the screen test (randomized complete blocks) will permit tests of fertilizer and other treatments to hasten flowering of surviving plants.

PROCEDURE

PHASE I. - MASS SELECTION AND FIELD SCREENING

Selection Criteria

Trees are selected only in areas of high rust infection in northeastern Minnesota. All sexually mature trees are selected if they have an adequate cone crop and are 45 years of age or younger. Since the rust was introduced into this area about 53 years ago, trees in age classes 45 or less may have been exposed to infection as seedlings and survived. Older trees that are apparently free of the disease, show evidence of having survived infection, or have cankers confined to branches are also considered eligible for selection.

Seed Collection and Propagation

Collection of about 1,000 seedlots is planned. Seed collections in 1966 and 1967 total about 500 seedlots; another 500 seedlots will be collected in autumn 1969. The plants are being propagated at the Eveleth Nursery through cooperation of the U. S. Forest Service.

Studies at the University of Wisconsin have demonstrated that there is an age-related rust-susceptibility factor that should not be ignored; the younger the plants the more susceptible they are. For this reason the plants will be grown to the age of 2-2 (2 years in nursery, 2 years in transplant beds) before transplanting to the test area.

Inoculation (Screening) Tests

Most previous tests of rust susceptibility of seedlings or clonal lines have been done artificially in order to insure optimum conditions for infection. One possible result of such intensive treatments is that they may far exceed any natural epidemic conditions and result in multiple infections that may cause the death of even highly resistant plants.

Screen tests in this project will be carried out under optimum natural conditions in a high infection area on the Tofte District, Superior National Forest. Since most ribes (*Ribes* spp.) plants now on the test area will be destroyed during site preparation, plants of the eight native and two naturalized species are being propagated and will be established on the test area at the time of initial outplanting.

Site Preparation and Planting

The test site is an area of 270 sq. chains. Most of the area was covered by a heavy sod which had been control-burned and will be periodically cultivated until planted.

Spot treatment with simazine is planned around each white pine and ribes plant immediately after planting. Other chemical or physical weed control will be avoided unless necessary.

The first outplanting on the test site (using 4-year-old stock grown from 1966 and 1967 seed) will be made in spring 1972; the final outplanting, using stock grown from 1969 seed, will be made in spring 1974.

In most mass selection programs, the seed is bulked before sowing in the nursery. In this study, identity of the "mother-tree" lines has been maintained in the nursery. The lines will be evenly distributed throughout the test site using a randomized complete block design with 1-tree plots. Identity of the seedlots beyond this point will not be maintained.

The planting will consist of 100 blocks or replicates, each block containing 1,000 plants. One-half of each block will be planted in 1972, the other half of each in 1974. Planting will be on 3x3 ft spacing in anticipation of high early mortality from rust infection.

To protect the plantation from fire loss, each group of 10 or 20 blocks (replicates) will be surrounded with firebreaks. A deer-proof fence with a minimum life of 15 years will surround the plantation. The fence will be installed in 1971.

Treatments to Hasten Flowering

Effects of fertilizers, interspecific grafting, and possibly other treatments to hasten flowering will be tested on a few replicates. Successful treatments will be applied to surviving trees in the screen test. Favorable results of such treatments would shorten the time to Phases II and III.

PHASE II. - ESTABLISHMENT OF CLONAL SEED ORCHARDS

This phase of the project will be initiated as soon as sufficient flowering occurs among trees of the screen test. Seed produced by random crossing may be used for commercial planting but only a 12- to 15-percent genetic gain in rust resistance may be anticipated. This gain may, however, be augmented at this stage by selecting a small number of the best trees (rust free, vigorous and otherwise desirable), asexually reproducing them as clonal lines by grafting and establishing them in seed orchards. These orchards could be established on good sites outside the high rust infection zone (to reduce pollen contamination) and managed for seed production.

Although the primary objective of this phase would be to increase seed production for commercial use, there are important additional advantages: (1) establishing the best trees into clonal lines will insure survival of at least a good sample of the screened trees in the event some catastrophy eliminates the screen test planting; and (2) additional breeding material will be available for the production of F_1 plants in Phase III.

PHASE III. - FULL-SIB FAMILY SELECTION AND RECURRENT SELECTION

This phase of the project will be initiated concurrently with Phase II, in about 15-20 years.

Selected screen test trees will be crossed and their offspring, identified by parentage, will be established in a replicated progeny test in a high infection zone. As these full-sib families reach sexual maturity, surviving family lines will be rogued of the least promising individuals. In terms of rust resistance, this will mean elimination of individuals that are severely cankered but survived. Selection at this stage may also favor the most vigorous or otherwise desirable individuals that show high resistance to the rust.

Open-pollinated seed produced by the selected trees of this F_1 generation may then be used commercially. Bingham and his associates (Bingham, Squillace and Wright, 1960) working with western white pine realized rust resistance genetic gains of up to 30 to 40 percent from similar crosses; such gains may reasonably be expected in this program. Additional gains in the F_2 and subsequent generations in terms of rust resistance and other traits may be anticipated until the genetic variation in the population is exhausted.

The first replicated progeny test (F_1) will be outplanted in about 20 years (ca. 1988). This will require an area of about 10 acres, isolated from the Tofte screen test site but in an equally high infection area.

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FLOOR DISCUSSION

Neither of the authors could be present to present this paper; it was offered only in abstract form and there was no discussion.

A CEREAL BREEDER AND EX-FORESTER'S EVALUATION OF THE PROGRESS AND PROBLEMS INVOLVED IN BREEDING RUST RESISTANT FOREST TREES: MODERATOR'S SUMMARY

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As a moderator of the panel "Breeding Schemes for Mass Production of Forest Trees," it is my responsibility to summarize and comment on the various papers that have been given during this session. However, since I am also by chance the moderator of this final formal session of the NATO-IUFRO Advanced Study Institute you have left yourselves vulnerable to a general harangue which will touch on a number of different aspects of the overall forest genetics and breeding programs, which have been presented this past week.

Four years ago, when I was invited to participate in the NATO-N.S.F. Symposium at Pennsylvania State University - after more than 20 years without contact with forestry - I was very favorably impressed by the vast amount of information that had been obtained and the progress that had been made toward the development of improved varieties or strains of *Pinus* and *Populus* spp. This week I have been even more impressed by the reports on progress since the last meeting. The first tangible results of the forest tree breeding programs are beginning to make their first commercial impact on southern pine pulpwood production. The *Pinus monticola* Dougl. white pine blister rust resistance breeding program is approaching the pay-off stage.

I have been greatly impressed also during the past five days by the high quality of the research reported from the disciplines of genetics, entomology, pathology, epidemiology, physiology, ecology, and taxonomy. Such work lays the foundations upon which your breeding programs must be built.

I take this opportunity to congratulate all of you on the tremendous progress already achieved. However, I urge you all to discard your modesty and conservatism and recognize the importance of the work which you are doing, not only for its direct effect on increasing the production of wood and fiber, but for its indirect effects on our total environment, i.e., watershed, soil conservation, wildlife, and recreation. The time has arrived to establish clearly before governments, private industries (especially those utilizing forest products), and the general public the present and potential contributions of forest tree breeding programs to the welfare of the general public. Only through an aggressive approach of this type can forest genetics hope to obtain the financial support it must have to carry out its important work.

There is no time for complacency and preening over research progress. I urge those of you who are engaged in breeding *Pinus monticola* Dougl. and *P. strobus* L. to develop and release for commercial use a blister rust-resistant seed source or cultivar as soon as possible. Time is precious. There would be little place in the American market today either for a superior model of the buggy (horse-drawn carriage), or for a cultivar of blight-resistant American chestnut, *Castanea dentata* (Marsh) Borkh. The need for both has disappeared. These voids have been filled by the gas-propelled automobile and the native oaks, respectively. It therefore behooves all of you who have developed rust-resistant pine varieties - even though they are not perfect - to put them into use in our forests as soon as possible. Unless you do you will be trying to promote the use of an obsolete species 20 years from now. Time and again I have seen ultra-cautious wheat breeders test and retest promising wheat lines until they became obsolete. The main contribution of such a frustrated breeder is to help further expand the all-too-common sterile research bureaucracies. Don't let it happen to forestry breeding programs.

THE PHILOSOPHIC BASIS FOR AN EFFECTIVE BREEDING PROGRAM

I think we all agree that it is absolutely necessary to maintain the right balance between fundamental (basic) and applied research if the forest tree breeding programs are to be kept viable and productive. Beware, however, of falling into the trap which has swallowed up many of our cereal breeding programs, namely that of unconsciously equating fundamental research with *useless research*. The fundamental research in forest genetics that is justifiable should be relative to the continuing progress of the breeding program. Consequently, almost always the fundamental research worth doing will be that which is identified by a scientist who is deeply involved and frustrated by a barrier to progress that he has encountered in the applied aspects of the program. Applied research should never be regarded as a "nasty or dirty word" as is so often the base today in many of our over-sophisticated research programs, even though it is being carried out by foresters with sweat on their brows and pitch on their hands. If such snobbishness prevails the breeding programs will wither (Borlaug, 1968).

I agree wholeheartedly with the comment that was made this afternoon by Prof. Warren Pope "--that you should avoid unnecessary oversophistication in research programs designed to breed rust-resistant pines." *Cronartium ribicola* J.C. Fisch. ex Rabenh. will not respect highly sophisticated plans which threaten its survival, if they ignore the genetic variability of the rust. The pathogen will then respond by circumventing the intended barrier to further frustrate the scientist. It has survived the quirks of nature over millions of years of tumultous geologic and ecologic changes and it will not be pushed into extinction by a few either oversophisticated or dirty-handed scientists.

Nor would I advocate the unwise use of inadequate scientific data which is fed into the latest model computer to give it scientific sanctification. This is a poor substitute for reliable data developed from critical observations of large populations of seedlings or trees, obtained with sweat from the scientist's brow, interpreted by that rare commodity - common sense, and even, if and when necessary, tabulated and summarized by hand.

WHAT IS THE CORRECT BREEDING MODEL FOR INCORPORATING RUST RESISTANCE INTO PINES?

The long period between germination and harvest of a forest species such as *Pinus monticola* Dougl. or *P. strobus* L. (i.e., 60 to 100 years) is one of the greatest obstacles confronting the forest tree breeder. Currently he has virtually no experimental data to determine the relationship of seedling or early sapling growth rate and form to the growth rate and form of the tree during the latter part of its silvicultural cycle. In the case of breeding for rust resistance he is in an even worse dilemma because of the difficulty of determining the effective longevity of the resistance. Will the rust resistance he is incorporating into his breeding material today lose its effectiveness before the tree reaches merchantable age? Or, will it provide adequate protection through the current cutting cycle and be transmitted effectively through its seed to protect the progeny for several forthcoming generations, or perhaps indefinitely? If the source and level of resistance that has been chosen is adequate, how can it be incorporated most rapidly and utilized most effectively to provide the best and most stable protection from rust over the longest possible period of time? These are but a few of the many imponderables that confront the forest tree breeder.

THE MODEL FOR BREEDING RUST RESISTANT FOREST TREES

I wholeheartedly agree with the points of view that have been expressed during this symposium (and in recent publications) by Bingham, Schreiner, Heimburger, Hoff, McDonald, Hattemer, Patton, Zobel, Kinloch and others that successful breeding for rust resistance in long-lived forest trees should be based on the accumulation of polygenes in a general (uniform or horizontal) type of resistance. Dr. J. C. Zadok's statement in these proceedings that, "The use of polygenes in breeding for partial resistance is 'nature's own method' and it is possibly the fastest and safest way to improvement," is certainly apropos.

Frankly, however, I am both confused and considerably concerned with the schizophrenic nature of the philosophy supporting many of the forest breeding programs. Many pay lip service to using general (polygenic horizontal) resistance (Caldwell, 1968), but simultaneously look over their shoulder and flirt with the use of specific, oligogenic, monogenic, hypersensitivity, or vertical resistance. There seems to prevail a fear that although general (horizontal) resistance is the rational approach, it may not be adequate or may not persist and that adequate protection may yet be found in specific resistance. Presentations and discussions at this symposium have evolved largely around specific resistance, although it has failed miserably to provide stable, long-lasting resistance in wheat, oats, and flax (van der Plank, 1968). I can personally attest to the futility of using it in forest tree breeding programs, *where it may be even less dependable*. Don't emulate the wheat, oat, or flax breeders, but instead, as I have previously suggested, adopt the methods of the maize breeders (Borlaug, 1958 and 1966).

Flor's hypothesis, based on the existence of a gene-for-gene relationship between the host and pathogen, appears to be valid for the specific rust resistance in self-pollinated plants. It does not necessarily follow, however, that this relationship holds for the quantitatively inherited polygenic uniform resistance in allogamous

(open- or cross-pollinated) species such as *Zea mays* L. (maize) and *Pinus* spp. Indeed there is much circumstantial evidence to indicate that this hypothesis is not valid in these cases.

Let us examine the soundness of the proposal to use general resistance in rust resistance breeding programs in *Pinus*. Maize and its corresponding rusts, I believe, provides the best model for such a study.

A CASE OF STABLE BALANCED BIOTIC RELATIONSHIP BETWEEN MAIZE AND ITS TWO RUST PARASITES

Maize (corn) is a monotypic species which apparently originated in the highlands of Mexico, Quatemala, and perhaps Peru, long before the beginning of recorded history. Archeological evidence indicates that about 7,000 years ago its wild forms were being used as food by the indigenous people of the area that is today the Valley of Tehuacan, Puebla, Mexico. About 5,000 years ago maize was being extensively cultivated in the same area (Mangelsdorf, MacNeish, and Galinat, 1968). It appears that the wild ancestors of maize became extinct perhaps because the pre-Aztecs did such an excellent job of "breeding and taming" the crop. Or perhaps if it still existed at the time the Spaniards arrived, the introduction of domestic goats, sheep, and cattle contributed their bit to its extinction.

Maize, like most of our forest tree species, is an open-pollinated species which has evolved into many geographic or ecotypic races, and subsequently into a much larger number of sub-races or varieties (cultivars).

Maize, throughout Mexico, Central America, and the highlands of northern South America was originally cultivated exclusively as open-pollinated varieties. Farmers modified the earlier existing types through mass selection to develop many varieties better adapted to their local needs. Even today open-pollinated varieties remain the basis of maize culture throughout most of Latin America, Africa, and Asia.

Two species of rusts parasitize maize throughout Latin America. *Puccinia sorghi* Schw. predominates at higher elevations and cooler temperatures, whereas *Puccinia polysora* Underw. predominates at the higher temperatures in lower elevations.

Although one or the other of these rusts is commonly found infecting nearly every plant of maize throughout its natural range in Mexico, Central America, and northern South America, the infection seldom occurs in sufficient intensity to cause appreciable damage, except rarely and locally, where some farmer (which is uncommon) or some scientist (which is more common) has upset the balanced biotic system which exists between host and pathogens.

Indeed there is no well-documented report indicating extensive epidemics of rust on maize in its native Latin American habitat either in colonial or in recent times. Undoubtedly the near perfect biotic balance between host and parasite has probably existed from the time maize was first domesticated, and almost certainly even prior to that time on its now-extinct wild ancestors.

THE EFFECT OF TEMPERATURE ON THE EVOLUTION OF MAIZE AND ITS TWO RUST PARASITES

Experimental and observational evidence indicates that the open-pollinated maize varieties currently grown in Mexico consists of 3 rather distinct groups of ecotypic races primarily differentiated by temperature (elevations). The 2 maize rust pathogens have evolved in an analogous way. *P. sorghi* prospers better at low temperatures and predominates at the higher elevations, where the maize varieties are resistant to this disease, but not to *P. polysora*. The opposite is true in the lowland tropics where *P. polysora* is predominant. At intermediate elevations both *P. sorghi* and *P. polysora* occur and there the maize cultivars in common use are resistant to both species (Schieber, Rodriguez, and Fuentes, 1964).

Apparently through the long process of evolution and natural selection the maize varieties grown in each of the 3 elevational zones have come into equilibrium with their rust parasites. So long as these balanced host-parasite systems are left undisturbed by man - scientist or farmer - the host exhibits a high degree of resistance to the rusts and suffers little or no damage.

Do not be misled into believing that the two species of *Puccinia* that parasitize maize are less pathogenic or less aggressive than those that attack wheat, oats, flax, or pine trees (Borlaug, 1966). Their pathogenicity becomes evident when the equilibrium between host and parasite is disturbed.

If the rust-resistant maize varieties, in either the temperate uplands or tropical lowlands, are inbred and tested in their native habitat, some lines will be developed which are killed by the rust while others remain resistant like the parent variety. Moreover, if one moves open-pollinated lowland maize varieties into the high elevations, they will rust severely. Similarly, when high elevation maize varieties are sown in the tropical lowlands, they are seriously infected. However, if the tropical varieties that rust severely at high elevations are inbred and the lines are evaluated at the high elevation sites, it will be found that some inbred lines can be isolated which show good levels of rust resistance. The same phenomenon is observed when inbred lines are developed from high elevation varieties and tested in the lowlands. The varieties from the intermediate elevational zone, however, can be moved either into higher elevations or lower elevations and still retain a high level of rust resistance.

Such experiments indicate that polygenes for general resistance to the 2 species of rusts exist in all varieties of maize in each of the three elevational zones, but that the varieties differ in the frequency of genes for resistance to the 2 species depending upon elevation. A high frequency of polygenes for resistance to *P. polysora* exists in lowland maizes whereas these same varieties possess only a low frequency of genes for resistance to *P. sorghi*. The opposite is true for the high elevation maize varieties. The maize varieties of the intermediate elevational zone have a high frequency of genes for resistance to both *P. polysora* and *P. sorghi*.

Although *P. polysora* and *P. sorghi* are similar in their physiology and host range, they are characterized by distinguishable differences in spore morphology and temperature responses. These phenomena challenge one to speculate whether a similar process may have been involved in differentiating *Cronartium quercuum* (Berk.) Miyabe and *C. fusiforme* Hedgc. and Hunt ex Cumm., although in the latter case the temperature gradient may primarily be due to differences in latitude rather than in elevation (Hooker, 1967; Peterson and Jewell, 1968).

Maize has also evolved into geographic races based on latitude. These many different sub-races and varieties each have their corresponding balanced populations of the two rusts. When varieties of maize which are resistant to *P. polysora* in El Salvador are planted in similar temperature elevational zones in Mexico, the introduced varieties, although resistant, will be somewhat more susceptible than the Mexican varieties. The same will be true of *P. sorghi*-resistant varieties of maize from the highlands of Colombia when they are sown in Mexico or when Mexican varieties are sown in Colombia. In all cases, however, there is a significant level of general resistance to the rust population in the "introduced varieties".

From these observations it is clear that a host-parasite equilibrium, based on general resistance, is established on the basis of both latitude and elevational environments resulting in harmonious survival of host and pathogen with little damage being done to either. So long as this equilibrium is not disrupted, losses to the corn crop are minimal, if not inconsequential.

PERSISTANCE OF QUANTITATIVELY INHERITED POLYGENIC RESISTANCE IN AFRICAN MAIZE VARIETIES IN THE ABSENCE OF SELECTION PRESSURE FROM *PUCCINIA POLYSORA*

Introductions of maize from the Caribbean islands, Mexico, and Central America, presumably highly resistant to the 2 rusts, were made into West Africa during the late 1400's and early 1500's. Apparently *P. sorghi* was inadvertently introduced into that region at about the same time and persisted in a balanced biotic system on maize, without causing serious crop damage, just as it had evolved and persisted in its native home in the Americas. For some inexplicable reason *P. polysora* was left behind in the Americas, and African maize culture evolved and remained free from this disease until perhaps the 1940's.

Suddenly, in 1949, a serious epidemic of rust on maize caused by *P. polysora* occurred in Sierra Leone, West Africa. Presumably the rust had been introduced into Africa from the Americas, perhaps on husks of roasting ears via airplane transport. Within 3 years this epidemic spread across the entire tropical maize belt of Africa and even as far as the islands of Mauritius and Reunion in the Indian Ocean, east of Madagascar. Somewhat later *P. polysora* epidemics broke out in Malaya, in Borneo, in Siam, the Phillipines, Christmas Islands, New Guinea, and Australia (Stanton and Cammack, 1953; Storey *et al.*, 1958; Van Eijnatten, 1965). Severe rust occurred over a wide area from 1950 to 1952 in tropical Africa, causing serious reduction in the maize harvest and provoking fears of famine and soaring grain prices. Estimates in many areas placed reduction in harvests at 50% or more (Van Eijnatten, 1965).

Several governments that had never before made any expenditure to improve the varieties of maize appointed scientists to study the problems. They began importing experimental maize seed from other parts of Africa, Asia, the U.S.A., the Caribbean, Mexico, Central America, and northern South America. All of the African and Asiatic varieties were found to be completely susceptible. The varieties from the U.S.A. were found to carry considerable resistance, whereas the varieties from the Caribbean area, Mexico, Central America, and northern South America were found to be highly resistant. With this data African scientists set about transferring to the African varieties a number of genes for hypersensitivity resistance that had caught their eye in the Caribbean and Mexican introductions (Stanton and Cammack, 1953; Storey *et al.*, 1958; Van Eijnatten, 1965).

Curiously enough, the rust epidemics in African varieties began to abate within 3 years after the first severe outbreaks developed in an area. The reduction in severity of the epidemic took place before the new, rust-resistant varieties being developed by scientists could be multiplied and distributed. Apparently, this resulted from an increase in the general reistance in the African varieties brought about within 3 years under the strong selection pressure of the pathogen under severe epidemics, but almost certainly also with the assistance of the peasant farmer. Under the strong selection pressure of 3 successive epidemics, the polygenes for general resistance that had been widely dispersed in the maize population during the 400 years that the African varieties had been grown in the absence of *P. polysora* were brought back together to stem the tide of the epidemic and to restore biotic balance between the host and pathogen (Van Eijnatten, 1965; van der Plank, 1968).

Unfortunately no one made observations on the frequency of effective or partially effective resistance genes in the African varieties when the epidemic began. Consequently a unique opportunity was lost to study the survival of genes for general rust resistance in the absence of selection pressure in random mating maize populations. Nevertheless, it is clearly evident that, despite separation of host and pathogen through 400 generations in the host and 10,000 generations in the pathogen,[1] the polygenes that were present in the original African varieties were still functional against the organism when brought back together.

I firmly believe that this evidence on the long-time persistance and stability of general resistance is of great significance to population geneticists and to all plant breeders, but especially to forest geneticists who are engaged in breeding long-lived blister rust resistant Pinus monticola *and* P. strobus.

I do not wish to imply that specific or hypersensitivity resistance has no place in plant breeding. It may be very valuable if used in combination with polygenic general resistance. When this is being attempted special precautions must be taken to avoid the loss of the polygenic system due to the masking or "vertifolia effect" of the hypersensitivity. Although the rust-resistant, open-pollinated maize varieties

[1]*Assuming one generation of maize culture, and twenty-five generations of* P. polysora *each year.*

of Mexico, Central America and the Caribbean are largely protected from rusts by general resistance, some varieties have been shown to possess associated hypersensitive genes (Hooker, 1967; Storey *et al.*, 1958; Ullstrup, 1965; Van Eijnatten, 1965).

The short period of usefulness of the specific or hypersensitivity resistance in wheat and oat varieties has been primarily due to the exclusive or near-exclusive use of this type of resistance genes, with a corresponding neglect for bringing together polygenes to provide general resistance as a base upon which hypersensitivity resistance can be superimposed. There is no doubt that a partially effective general resistance to stem rust of wheat (*Puccinia graminis* f. sp. *tritici* Eriks. & E. Henn.) based on polygenes, exists to a certain extent in such wheat varieties as Hope, H44, Yaqui 50, Selkirk, Bonza 55, and Penjamo 62. *The spectrum of polygenes in such varieties should be increased.* There are, however, more difficulties encountered in trying to incorporate and concentrate, as well as maintain, a large "dosage" of these types of rust-resistance genes in an autogamous crop species such as wheat, contrasted to an allogamous crop species such as maize, or pines.

THE EXISTENCE OF "FOSSIL"[2] GENES CAPABLE OF CONTROLLING BLISTER RUST IN *PINUS MONTICOLA* AND *P. STROBUS*, A HYPOTHESIS[3]

The chestnut blight organism *Endothia parasitica* (Murr.)A. & A. indigenous to the Orient and endemic on Chinese hairy chestnut *Castanea mollisima* Blume was introduced into the U.S.A. at the turn of the last century. It found a very congenial host in the American chestnut *Castanea dentata*, which was then one of the most valuable components of the eastern forests. This species was destroyed as a commerical forest species throughout its range by 1940; susceptibility was complete and universal and not a single resistant tree was found. The complete absence of resistance is evidence that *C. dentata* had never before been in contact with the pathogen *E. parasitica*.

Currently the introduced Dutch elm disease caused by *Ceratocystis ulmi* (Buism.) C. Moreau is perpetrating a similar destruction of the American elm, *Ulmus americana* L. This pathogen was introduced from Europe in the 1930's, but is thought to have been originally endemic on *Ulmus pumila* L. in the Orient. Although it has already devastated and destroyed American elm over much of its natural range, no resistant trees have been identified. This is another case of an indigenous tree species being destroyed by a pathogen with which it had never previously been in contact.

[2]*The term "fossil" as used here, refers only to the antiquity of the genes as indicated by circumstantial evidence of the long persistance of the genes in the host population, in the absence of the selection pressure of the pathogen.*

[3]*When this hypothesis was developed the author was unfamiliar with the fossil evidence (reported by Hopkins* et al., *Vashkovsky, and Mirov indicating that* P. monticola *or a near relative once inhabited eastern Siberia. This evidence is summarized in an article now in press entitled* Genetics of Western White Pine, *by R. T. Bingham, R. J. Hoff, and R. J. Steinhoff.*

I have been greatly impressed with the progress that already has been made by R. T. Bingham and colleagues in breeding blister rust-resistant *Pinus monticola* through intraspecific crossing (Bingham, 1966). Similar progress has been achieved by C. Heimburger, and A. J. Riker and R. F. Patton in breeding for blister rust resistance in *P. strobus* by the intraspecific approach.

During the past 4 days I have been fascinated as the story of high levels of resistance to blister rust were reported by Søegaard, Gremmen, Bakshi, Heimburger and Bingham in *Pinus sibirica* Du Tour; *P. koraiensis* Sieb. & Zucc., *P. armandii* Franch., *P. parviflora* Sieb. & Zucc., *P. wallichiana* Jacks. (syn. *P. griffithii* McClell.), *P. peuce* Griseb. and *P. cembra* L.

Most interesting of all to me, however, are your reports that, in *P. monticola* and *P. strobus*, about 1 tree in 20,000 and 1 tree in 10,000, respectively, have survived the onslaught of the blister rust epidemics. Most of the phenotypically resistant trees that have been studied in detail have proved to be genotypically resistant, not escapes. Controlled crossing between genotypically resistant trees of *P. monticola* followed by progeny testing of the seedlings, has definitely established that an additive polygenic type of general resistance is involved.

All individuals in *Castanea dentata* and apparently also in *Ulmus americana* populations were uniformly susceptible to the introduced pathogens *Endothia parasitica* and *Ceratocystis ulmi* respectively, and both host species face extincion. This appears to be good circumstantial evidence that neither American chestnut nor American elm had ever been in contact with the corresponding pathogens before their recent introductions. By contrast, genes for resistance to *C. ribicola* are present in both *P. monticola* and *P. strobus*. WHY THE DIFFERENCE? Yesterday I made a statement that it appears to me you are dealing with "fossil" polygenes for resistance to *C. ribicola* in both *P. monticola* and *P. strobus*. How else can one explain the existence of polygenic resistance in these two species?

The genes for resistance to *C. ribicola* in *P. monticola* and *P. strobus*, although originally present at a low frequency and widely dispersed, are being brought back together successfully and increased in frequency through use of selection pressure of the pathogen in progeny tests following crossing. The resistance may be functional against the entire range of pathogenicity of *C. ribicola* currently present in Western North America. I hypothesize that these are "fossil genes" that have persisted in *P. monticola* and *P. strobus* since geologic time. These genes would not be present in these North American pines unless there had been previous contact between *C. ribicola* and *P. monticola* and *P. strobus*.[4] There is no way to predict accurately how far back in geologic time this host-parasite relationship existed.

Conifers are very old, but the fossil evidence supporting their antiquity is fragmented. There is evidence, however, from petrified forest fossils in several parts of the world, that conifers were well

[4]*Editor's note: Another explanation might be gene (pollen) exchange between the "resistant" Eurasian white pines and the progenitors of the 2 present North American species, even though they had not come into direct contact with the rust.*

developed by the Triassic period, some 230 to 180 million years ago (Moore, 1949). The fossil evidence on the age of the rust fungi is even more unreliable. Arthur (1929, p. 205) refers to a Miocene fossil (12 to 25 million years old) of *Phelonites lignitum* Fres., a rust on seed of *Glyptostrobus*, a coniferous genus once common, but not restricted to a single species in southeast China. He considers *Phelonites* similar to present-day *Cronartium* and postulates that the rust may have originated in the early Mesozoic Era, but admits this is based on speculation rather than on observational evidence.

What is the explanation for the presence in the American species *P. monticola* and *P. strobus* of the "fossil polygenic" general resistance to *C. ribicola*, a pathogen only recently introduced into North America? Presumably the center of origin of *C. ribicola* was in eastern Asia on Asiatic soft pine species. The pathogen is endemic there today parasitizing, but causing little damage to a number of species including *P. sibirica*, *P. pumila* Regel, *P. koraiensis*, *P. armandii*, *P. parviflora* (and forms) and *P. wallichiana*.

Similarly, in the mountains of the Central and Balkan European countries, which may be a secondary zone of differentiation of the pathogen, and which is also the area from which the pathogen was introduced into North America, *C. ribicola* lives in a balanced biotic relationship with *P. peuce* Griseb. and *P. cembra* L.

The circumstantial genetic evidence indicates it is highly probable that at some unknown time in the geologic past the range of the ancestors of modern *P. monticola* and *P. strobus* overlapped with those of one or more of the Asiatic soft pine species on which *C. ribicola* was then endemic (Moore, 1949; Ogburn, 1970). Thus, the ancestors of present day *P. monticola* and *P. strobus* likely came under infection and the selection pressure of the pathogen and responded by evolving into species with polygenic general resistance to *C. ribicola*. Before the Bering land bridges disappeared between what is today the Asian continent and North America, the predecessor of *P. monticola* had extended its range to the latter continent. One can conjecture either that, for some inexplicable reason, the pathogen was left behind in Asia (as was the case 400 years ago when *Zea mays* and *Puccinia sorghi* were both introduced into Africa from the Americas, while the other rust pathogen *P. polysora* was left behind in America), or that more probably the pathogen was subsequently killed out on the American host at some later geologic period, perhaps during one of the glacial periods of the Pleistocene or some earlier ice age, during which the host, *P. monticola*, was able to survive, while the pathogen became extinct on the North American continent.

Consequently, we may conclude that once the polygenes for general resistance have evolved in an open-pollinated species they can persist indefinitely in a population in the absence of the selection pressure of the pathogen if they are not linked to other genes adversely affecting the survival of the host species. They will, however, become dispersed in the population and, until brought back together again under renewed selection pressure of the pathogen, may sometimes give the impression that the entire population is susceptible.

It appears to me that the circumstantial evidence supporting the above hypothesis implies that: (1) the pathogen *C. ribicola* is very ancient; (2) *P. monticola* and *P. strobus*, or their ancestors, and *C. ribicola* co-existed in a balanced host-pathogen relationship in the

geologic past, perhaps millions of years ago, and subsequently became separate; (3) the genes for pathogenicity in the pathogen, at least those derived from the European secondary zone of distribution of the organism, do not transcend the spectrum of the "fossil genes" for resistance in the long isolated host *P. monticola*; (4) the stability, longevity and effectiveness of the polygenic general resistance is circumstantially evident; once the dispersed genes are reshuffled and reconcentrated into modified populations of the host through the exertion of strong selection pressure by the reintroduced pathogen, they can again provide adeqaute protection against *C. ribicola*.

VARIABILITY IN *CRONARTIUM RIBICOLA* AND ITS IMPLICATIONS IN ORGANIZING THE BREEDING PROGRAMS

There is no doubt but that great variability in pathogenicity exists within *C. ribicola*, as has been found in all other rust fungi which have been studied in detail. There is considerable circumstantial evidence in Europe and Asia that different races of *C. ribicola* predominate in different geographic areas. How else can one explain the differences in the relative rust resistance of the various soft pine species when they are grown in several widely separated geographic areas where they come into contact with different sources of wild inoculum? This has given rise to much confusion in the literature concerning the relative resistance of the different soft pine species and their relative merits as parents. In this respect the situation is no different than that with *Cronartium fusiforme* on *Pinus elliottii* Engelm. and *P. taeda* L. in southern U.S.A. Progeny grown from seed collected from several widely separated areas of both of these pines exhibit considerable differences in reactions to the fusiform rust pathogen when they are grown in contact with wild inoculum of the fungus at different locations (Peterson and Jewell, 1968; Kais and Snow, and Powers, these proceedings.

Yesterday in the nursery we were shown convincing evidence by McDonald and Hoff of the existence of two and possibly three different races of *C. ribicola*, based on different needle-lesion types on the needles of pine seedlings. There is little doubt but that many more could be identified. *I would, however, discourage you from dissipating your limited research budgets and precious scientific manpower on such a sterile research effort. Do not copy the rust race identification work on the self-pollinated crops like wheat, oats and flax. This should not be your model!*

In maize, resistant varieties and hybrids with effective, stable, largely general resistance to *Puccinia sorghi* and *P. polysora* have evolved or have been bred without resorting to the identification of races. It is true a few scientists have identified races of these rusts by the use of varieties with hypersensitive genes (Stanton and Cammack, 1953; Storey *et al.*, 1958; Ullstrop, 1965). These genes, however, have not been used to develop rust-resistant varieties, with the possible exception of certain African countries. In most American maize varieties resistance is attributable largely to polygenic general resistance which can be manipulated in breeding programs without resorting to the largely sterile taxonomic exercise of race identification.

All that is necessary to effectively breed and screen for resistance against pine rusts, assuming that your breeding materials are carrying effective genes for resistance, is to use wild cultures of the rust

organism that adequately cover the spectrum of pathogenicity of the pathogen throughout the region for which the varieties or cultivars are being bred, and that can penetrate through any specific resistance that may be present. Beware of using wild inoculum from only one local area close to your research center. It may not represent the entire spectrum of the pathogenicity of the pathogen. Have no fears of bringing in wild inoculum for your screen tests from remote areas of your region. If your breeding stocks fall prey to such inoculum it simply means that the genetic base for resistance in your breeding program is too narrow to provide effective protection for a long cutting cycle species such as *P. monticola*, *P. strobus* (60 to 80 years) or even for short cutting cycle species such as *P. taeda* or *P. elliottii* (25-40 years). One must remember it took *C. ribicola* only about 40 years to spread over most of the range of *P. monticola* even with the *Ribes* eradication programs trying to hold the spread. Moreover, it is absolutely necessary to obtain the inoculum from a broad spectrum of species and varieties of the alternate hosts (i.e., *Ribes* spp. or *Quercus* spp.) to minimize the danger of using too narrow a spectrum of pathogenicity of the rust.

Rust tests designed to determine the general resistance of progeny must take into consideration: (1) The dosage of inoculum used, (2) the amount of infection produced, (3) the amount of inoculum produced, and (4) the rate of disease spread in host tissue. The inoculation test should measure the biotic balance between the host and pathogen.

Valvilov[5] (1935) long ago pointed out that the greatest diversity and widest spectrum of genes for pathogenicity of an obligate parasite, such as *C. ribicola*, as well as genes for resistance in the host, are found in the center of origin of the pathogen, which in this species is most certainly eastern Asia. *C. ribicola* is also almost probably more variable in its secondary zone of differentiation in Europe than it is in North America. It is possible that only a part of the spectrum of pathogenicity was introduced into North America from Europe. Nor is there any assurance that the culture of *C. ribicola* introduced into western U.S.A. and now decimating *P. monticola* is the same as that introduced into eastern U.S.A. on *P. strobus*. Perhaps rust culture differences in part account for the apparent lower level of effective protection provided by the intraspecific rust-resistance breeding programs on *P. strobus* as contrasted with that in *P. monticola*. The short period of time that *C. ribicola* has been present in North America - 60 to 75 years - probably has been too short a period to contribute much to its diversification since introduction.

All of the aforementioned considerations have important bearings on the choice of sources of parental resistance and on the evaluation of the effectiveness of resistance in current breeding programs. A forest tree breeder could proceed with great confidence if he knew that his parental stocks were resistant to *C. ribicola* in 5 or 6 areas in eastern Asia where the pathogen is indigenous and endemic, in several locations in the secondary zone of differentiation in Europe, as well as in the region where he is conducting his breeding program.

[5] *Vavilov's hypothesis probably was largely formulated to apply to resistance provided by genes causing hypersensitivity in the host (specific resistance). It may, however, also apply at least in part to polygenic general resistance.*

Since parental breeding materials of pine can be propagated vegetatively either through grafts or rooted cuttings, this type of world-wide information could be developed much more easily and effectively than with a crop such as maize.

All that is needed to achieve this vital background information with which to guide the breeding programs is the imagination, vision, determination, and cooperation of a group of forest geneticists, pathologists, and breeders (such as are represented here today), dedicated to combining their efforts to fight for the development of several sites for International Cooperative Testing in the areas of the world where white pine is important or could become important and where the pathogen exists.

PROGRESS ACHIEVED IN BREEDING RUST-RESISTANT PINES

IMPROVEMENTS IN SOUTHERN PINES

Cronartium fusiforme, the pathogen causing southern fusiforme rust, is endemic on a number of southern pine species, including the important loblolly *(Pinus taeda)* and slash (*P. elliottii*) pines. Presumably in the undisturbed southern forest a balanced host-parasite relationship existed, as it does today in the little-disturbed western forests of lodgepole pine, *Pinus contorta* Dougl., and the western gall rust pathogen *Peridermium harknessii* Moore, where little damage is done to the host.

The equilibrium between host and pathogen - between loblolly and slash pines and *C. fusiforme* was undoubtedly first seriously disturbed when logging operations 50 to 100 years ago removed all the merchantable trees and left standing young non-merchantable trees. Unfortunately the logging operation also left many large cull trees, including many seriously galled or cankered by the rust fungus. The cull trees often constituted much of the pollen source for the younger trees, and this resulted in an increased rust problem on seedlings grown from such seed. The problem was further aggravated during the economic depression years and the war years (1930's - 1945) when much abandoned agricultural land was converted to slash and loblolly pine plantations. Seed was in great demand and sources were not controlled. Much of the seed was probably obtained from rust-susceptible trees of bad form. As a result, by the end of the war many of the young plantations of loblolly and slash trees were of bad form and/or seriously rusted.

Aggressive forest tree improvement programs were organized in the mid 1940's, through the cooperation of universities, state governments, the federal government and forest product-utilizing industries. The results have been spectacular. Improved control of the seed sources of both loblolly and slash pine are already paying big dividends by increasing both the level of rust resistance and improving the growth rate and the tree form. Perhaps the regeneration - both natural and plantation - originating from improved seed sources has already achieved a level of rust resistance considerably over what it was 25 years ago. Moreover, seed from progeny-tested seed orchard trees is now rapidly becoming available. This seed will give another increment in rust resistance probably raising it to an average level that will be higher than that which was present in the undisturbed virgin forests, and will also simultaneously contribute to further improvements in growth rate and tree form.

The excellent programs in genetic improvement of loblolly and slash pine being done in North Carolina, Georgia, and Florida have demonstrated clearly how the imbalances between an indigenous pine host and an indigenous rust pathogen that have been provoked by man using bad timber management practices, can be brought back to the original level of the undisturbed forest or even further improved while concurrently improving growth rate and tree form.

IMPROVEMENT IN *PINUS MONTICOLA*

Intraspecific Rust Resistance

The accomplishments of R. T. Bingham and colleagues toward the development of blister rust-resistant western white pine through intraspecific breeding during the past 20 years have been spectacular, if not phenomenal. They have identified more than 3,100 widely dispersed trees of *P. monticola* that are phenotypically resistant to *C. ribicola*. Some of the phenotypically resistant trees have been inoculated as grafts and have also been found to be genotypically resistant. *They have in effect dug up "fossil" additive polygenes for resistance to* C. ribicola *where there should have been none based on previous ideas and experiences.* They have made controlled pollination test crosses and tested the F_1 progeny of more than 400 of these trees, and identified approximately 100 individual trees which are good general combiners for rust resistance. Pilot-scale seed orchards have been established employing grafts of the best of these trees, the first of which are now beginning to produce F_1 seeds. It is estimated that 30% of the F_1 seedlings will be resistant to blister rust. And in their main, first-stage seed orchard program, F_1 seedlings that have survived inoculation are being planted in production seed orchards, to mass-produce presumably 50±% resistant F_2 seedlings beginning about 1985. This is a tremendous accomplishment. We all salute you for your achievements. Their second phase plans call for expanding the base of the resistance already in use and diversifying the sources of rust resistance.

I would like to make a few comments concerning this phase of the breeding program. I think it is urgent to evaluate the remaining 2,700 phenotypically resistant trees as soon as possible so that other newly identified resistant trees can be incorporated into the seed orchards and thereby expand the genetic base of the current breeding program. *This will probably provide additional genes for protection, but even more important will reduce the chances of encountering other unforeseen problems with insects or other diseases that are of no consequence in the present* P. monticola.

Interspecific Crosses to Transfer Blister Rust Resistance to American Soft Pines

Although excellent progress has been made toward developing blister rust-resistant *P. monticola* through intraspecific breeding, there is an urgent need for widening and deepening the spectrum of resistance through interspecific crosses with the resistant Asiatic and European white pine species. Crosses with the Asiatic and European species will not only further diversify the gene pool for resistance to *C. ribicola* but may simultaneously incorporate other valuable genes into *P. monticola* (or *P. strobus* and *P. lambertiana*).

Carl Heimburger (these proceedings) has given an excellent summary of his many years of work on intercrossing the American species *Pinus strobus*, *P. monticola*, *P. lambertiana* Dougl., *P. albicaulis* Engelm., and *P. flexilis* James with the Asiatic species *Pinus wallichiana*, *P. parviflora* (including *pentaphylla*), *P. armandii*, *P. koraiensis* and *P. sibirica* and the European species *Pinus peuce* and *P. cembra*. Although he has reported partial sterility, manifested by a lower cone set and lower set of full seed per cone than in intraspecific crosses, he has nevertheless successfully made many new interspecific crosses which definitely open the door to the diversification and enrichment of the gene pool for resistance to the blister rust pathogen.

In the course of these studies, he has also made two other discoveries of great potential value to forest genetics. These include (1) the discovery of a gene (or genes) in *P. peuce* for early flowering, and (2) the discovery of a gene (or genes) in *P. peuce* for resistance to the white pine weevil, *Pissodes strobi* Peck, one of the principal enemies of *P. strobus*. Both of these discoveries are of profound potential importance to future pine breeding programs.

The dominant gene for early flowering has been transferred to several other species in crosses and generally reduced the period required for abundant flowering from 25 years, the normal for *P. strobus*, to from 5 to 7 years in the hybrids. This great saving in time removes one of the principal barriers that has confronted forest geneticists in the past. *I urge you to use such genes imaginatively and aggressively without fear that early flowering automatically means early senescense.* Moreover, it is inevitable that we will be utilizing shorter cutting cycles for all species in the future than we have in the past. We will be less concerned about the growth rate of *P. strobus*, *P. monticola* and *P. lambertiana* beyond 80 years, for most cutting cycles with these species will probably be of 60 to 80 years.

Henry Gerhold now has the interesting challenge of producing an improved *P. strobus* with resistance to both weevil and blister rust. He has the opportunity to first combine the weevil resistance of *P. peuce* with that which is apparently already present in *P. strobus*, and either simultaneously or subsequently combining the weevil resistance with rust resistance. To achieve this objective close cooperation will be required between entomologists, pathologists, and breeders. Effective methods will be needed for screening large numbers of seedlings for resistance to both weevil and rust. Whether an attempt is made to develop lines which from the outset combine resistance to both pests, or to develop lines with resistance to rust and others with resistance to weevils and subsequently combine them through convergent crosses, will probably depend largely upon whether or not there are lines of *P. strobus* available now with a good usable level of rust resistance. If such lines are not available then the latter approach is the only feasible one.

MUTATION BREEDING

S. Kedharnath has given an excellent summary of the present status of mutation breeding. I again caution you, just as I did 4 years ago, not to look for magic in this sophisticated approach to plant breeding. Where there are *unexploited known genes for resistance* present in nature, as is the case with *C. ribicola* or *Pissodes strobi*, why dissipate your limited budgets on such sophisticated approaches until these genes have been utilized. Although there have been hundreds of scientific articles published on the anticipated contributions of mutation breeding to the improvement of crop plants during the past 20 years, the accomplishments have at best been very modest *if not insignificant*. Most of these research efforts have produced nothing worthwhile. It is my contention that had the amount of money that has been spent on mutation breeding been spent instead on conventional breeding, much more would have been accomplished.

CONCURRENT IMPROVEMENT OF DISEASE RESISTANCE AND OTHER CHARACTERS

Ernst Schreiner (1969) has forcefully stated the need for concurrent improvement of growth rate, product quality, and disease and insect resistance. I concur that this is not only desirable but feasible if the breeding program is properly organized. To achieve this objective it is absolutely necessary to develop a broadly based gene pool, and grow and study large populations. The development of a diversified gene pool must begin with the selection of a large number of superior parent trees of the variety or species which is to be improved. All too often the number of parent trees is too small, and consequently the genetic base is too narrow to permit multiple character improvement. The selection of these parent trees should be done not only on the basis of disease and insect resistance but should also take into consideration rapid rate of growth, good tree form, and a wide breadth of adaptation. Similarly when interspecific crosses are to be made to transfer disease resistance, i.e., rust resistance, the "donor" parent trees should be selected not only for their outstanding resistance but also, insofar as possible, for a good combination of other desirable silvicultural characteristics.

Although provenance tests of many of the most important forest tree species have clearly established the existence of ecotypic races that differ widely in silvicultural characteristics, the genetic implications of these differences are all too often ignored when breeding programs are being organized. Currently in most forest tree breeding programs the genetic base on which the program is being built is extremely narrow, much more so, for example, than in maize breeding programs. All too often breeding programs have been based upon a few dozen or at the most a hundred parent trees. Is this an adequate sample of the genetic variation that occurs in a species that may cover a range varying from 500 to 1,000 miles, and may include tremendous variations in elevation, latitude, and sites?

The situation is even more unrealistic in the choice of parent trees of exotic donor species. Frequently a very few trees, one to several, generally growing in an arboretum have been used as being representative of a species. Often such donor species occupy vast forest areas in remote parts of the world. Are these parent trees adequate samples upon which to build viable, long-range breeding programs? Regardless of the accuracy and sophistication of the population genetics that are employed

in a breeding program to calculate heritability and genetic gain, it will be of no value unless wise, adequate sampling is done to select superior parent trees in the main provenances of the species that is to be improved.

Once a proper choice of parental trees has been made, an aggressive crossing program must be launched to develop a widely diversified gene pool. Large populations of seedlings from this diverse gene pool must be grown and screened economically if the program is to be successful. The nursery screening tests for rust resistance, which we observed yesterday at the Intermountain Forest and Range Experiment Station nursery, are an excellent example of an effective first screen. I caution, however, against employing nursery test methods that are designed to identify and save only seedlings with hypersensitivity. Seedlings that survive the nursery screen test should be transplanted to a regional performance nursery located in a high infection area (*in an ecological environment conducive to heavy infection*), where rust infection can be intensified by the extensive interplanting of many species of *Ribes*. Aeciospores from many different parts of the region should be used to infect the *Ribes*. The regional performance nursery approach proposed by Pauley and Ahlgren (these proceedings) would certainly be a good second screen.

The outstanding saplings which emerge from these two types of tests, and which are candidates for use in seed orchards, should be evaluated, whenever possible, for disease and insect resistance, winter hardiness, growth rate, tree form, and general adaptation in regional, national, and international tests. Species such as pines that can be propagated vegetatively through grafting or cuttings lend themselves to simultaneous testing at many sites much better than do crop plants. The use of a widespread network of national and international testing sites will not only assist in selecting individual trees with unusual disease and insect resistance, but can also lead to the identification of trees with an unusually broad range of adaptation.

APPLICATION OF THE ABOVE PRINCIPLES IN CEREAL CROPS

Before closing I would like to show you how some of these principles have been employed in the Mexican - CIMMYT[6] wheat breeding program during the past 10 years to revolutionize wheat production in a number of different countries. The wide adaptation of the Mexican varieties is not accidental, but the result of methods used in their development. The results have destroyed many of the former plant breeding concepts that placed much emphasis on the importance of tightly fixed variety-environment interactions which precluded the development of widely adapted varieties. The current results clearly indicate the advantages of broadly adapted varieties with built-in stability for grain yield over a wide range of conditions (sites, elevations, latitudes, and season). I predict that, if a sufficiently diversified gene pool is developed and if an adequate number of testing sites are employed, varieties or cultivars of maize and pines with amazingly broad adaptation can be developed similarly.

[6] *Centro Internacional de Mejoramiento de Maize y Trigo (International Maize and Wheat Improvement Center).*

THE DEVELOPMENT OF HIGH YIELDING BROADLY ADAPTED MEXICAN WHEAT VARIETIES AND THEIR EFFECT ON WORLD WHEAT PRODUCTION

From the outset in 1944 the Mexican Wheat Improvement Program, sponsored jointly by the Government of Mexico and The Rockefeller Foundation, was organized to develop high-yielding varieties with good resistance to diseases and which would be efficient in use of both irrigation water and fertilizer.

In order to shorten the time required to produce a new variety, against the advice of the experts, our program pioneered extensively in the growing of two generations of all breeding material each year. One generation was grown during the winter, the commercial wheat crop season, near Ciudad Obregon, Sonora, at about 28°N. latitude on the coastal plain only a few feet above sea level. Near Toluca a second generation was obtained by planting during mid-May at 8,500 feet and 18°N. latitude. The Toluca site is characterized by heavy rainfall throughout the growing season and cool temperatures. Consequently severe epidemics of both stem and stripe rust develop at this site every year.

The process used in the Mexican program of moving segregating populations over 10 degrees of latitude and from near sea level to 8,500 feet elevation, and its reverse, not only reduced by half the time required to develop a new variety, but also simultaneously permitted the identification of lines and the development of varieties with wide adaptation. We now know that this, at least to a large extent, is the result of the selection of lines that are insensitive to changes in day length and date of planting, and hence are broadly adapted. Other selection pressures also are undoubtedly acting under the very diverse conditions that prevail at these two nursery sites (Borlaug, 1968).

During the past 7 years CIMMYT has organized and coordinated The International Spring Wheat Yield Nursery which is currently grown by collaborators at more than 80 locations in the world. The varieties included in this nursery include representatives of all of the principal spring wheat producing areas of the world. During the past 7 years the Mexican varieties have exhibited uniquely broad adaptation as measured by high grain yield in many different countries of the world. Although they were bred for use under irrigation with heavy fertilization, some have shown outstanding performance under both fertilized and non-fertilized, irrigated and non-irrigated conditions.

During the past 3 years, the Mexican dwarf wheat varieties have been the principal catalyst involved in triggering off the green revolution in Pakistan, India and Turkey (Borlaug, in press; Borlaug *et al.*, 1969). They are now opening the breach to higher yield plateaus in a number of other countries. It is the unusual breadth of adaptation, combined with high genetic grain yield potential, dwarfness, a strong responsiveness to fertilizers, and a broad spectrum of disease resistance that has made the Mexican dwarf varieties so valuable to world agriculture. This revolution in wheat production was not based, however, on the panacea of the Mexican dwarf seed alone. It involved the transplant from Mexico to Pakistan and India of a whole new production technology that makes these varieties highly productive. Perhaps 75 to 80% of the research done in Mexico in developing the package of cultural practices, including fertilizer recommendations, was valid in Pakistan and India. Adaptive research done in Pakistan, India, and Turkey while the imported seed was being multiplied provided the necessary information to cover those gaps where the Mexican data were not valid.

The impact of the high-yielding, fertilizer responsive, light-insensitive, dwarf Mexican varieties on yield and production of wheat in Mexico, Pakistan and India is shown graphically in Figures 1, 2, 3, and 4. The Mexican varieties have made Pakistan self-sufficient in wheat production and have helped India take a giant step in this direction. It is estimated that they have increased the combined gross national product (GNP) of the two countries by 1.5 billion dollars during the past two harvests, compared to the 1965 base which was a previous all-time record crop (Borlaug, *et al.*, 1969).

Amazingly although the Mexican dwarfs were bred and developed for irrigated areas, they also are proving to be highly effective under rain-fed areas in many parts. Approximately 20% of the barani (rainfed) area sown to wheat in Pakistan is in Mexican dwarfs. Virtually all of the Afghanistan area sown to Mexican dwarfs and more than 80% of the Turkish area is rainfed. Next year about 20% of the entire area sown to wheat in Tunisia, virtually all of it rainfed, will be in Mexican dwarfs.

During the 1968-69 crop season, Mexican wheat varieties were grown on more than 20 million acres in foreign countries. This is more than 10 times the entire area sown to wheat in Mexico, the country for which they were bred. *Little did I realize, when we initiated the breeding program 25 years ago to assist Mexico to become self-sufficient in wheat production, that it would subsequently have a "world-wide" impact. Your forest tree breeding projects too will evolve into programs with world-wide impacts if you concentrate your efforts on valuable forest species, develop and maintain very diversified gene pools, and develop an international system of cooperative testing.*

THE MONSTER GROWS

The seriousness and magnitude of the world food problem must not be underestimated. The recent, much-publicized successes of the green revolution in increasing wheat, rice, and maize production in Asian countires only offers the possibilities of buying 20 to 30 years of time in which to bring population growth into balance with food production.

Plant breeders who look ahead must not be satisfied with maintaining the current yield plateau for our major food crop plants. Complacency can bring disaster.

The unrelentless pressure of exploding world population, with no relief in sight, should urge all of us to struggle to increase the potential yield levels of all food crops if we are to help ward off widespread world famine within the next 50 years.

I believe there is entirely too much conservatism in virtually all plant breeding programs. One of the first lessons which we learn in genetics is that maximum levels of heterosis and yield are generally obtained from crossing genetically distinct parents. This principle we promptly ignore in our breeding programs, with few exceptions. Most programs involve crossing closely related varieties or parents. Frequently this error is compounded by long backcrossing to the commercial parent. There is very little possibility of significantly increasing the grain yield potential in new varieties developed with these types of approach.

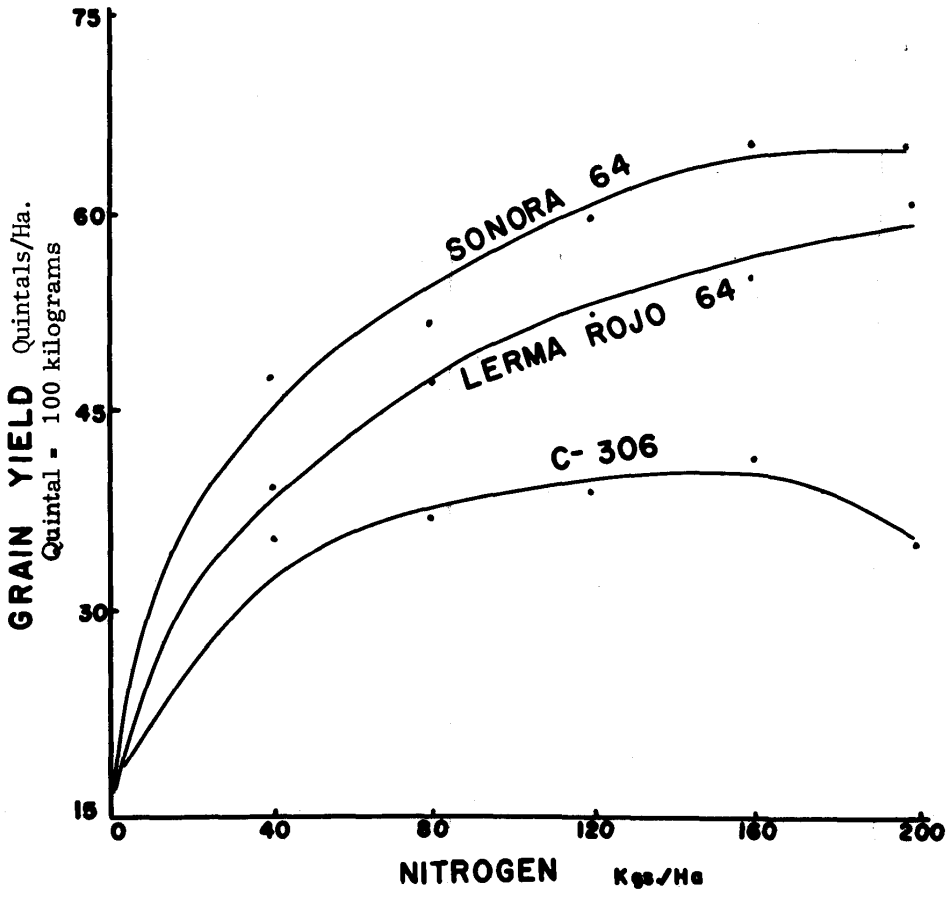


Figure 1. Differential nitrogen response curves for two Mexican dwarf wheat varieties compared to one of the best tall-strawed Indian varieties C 306, at the Uttar Pradesh Agricultural University, Pantanagar, U.P., India in 1966. Data by Drs. K. C. Sharma, D. Misra and B. C. Wright.

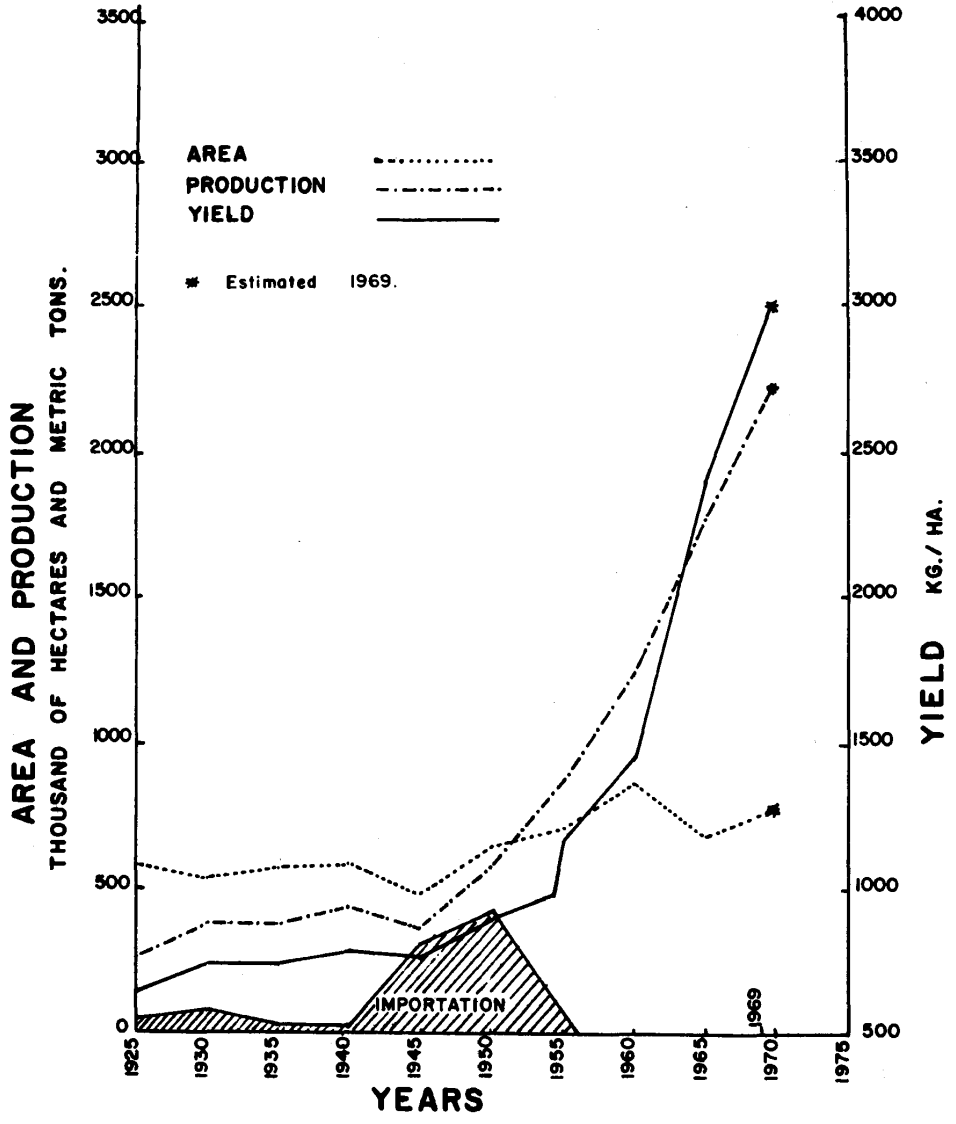


Figure 2. Cultivated area, production and yield of wheat in Mexico.

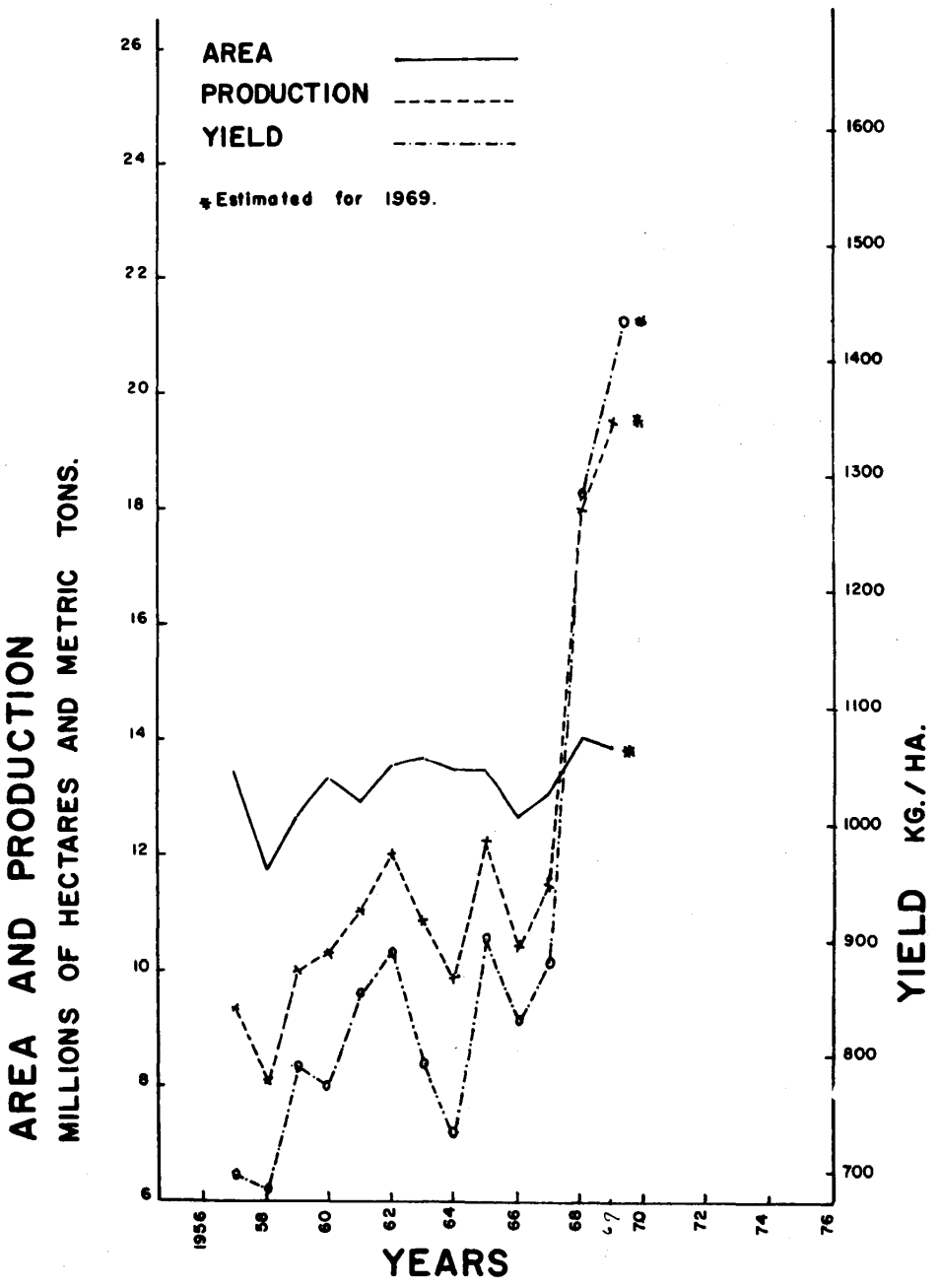


Figure 3. Total area; production and yield of wheat in India.

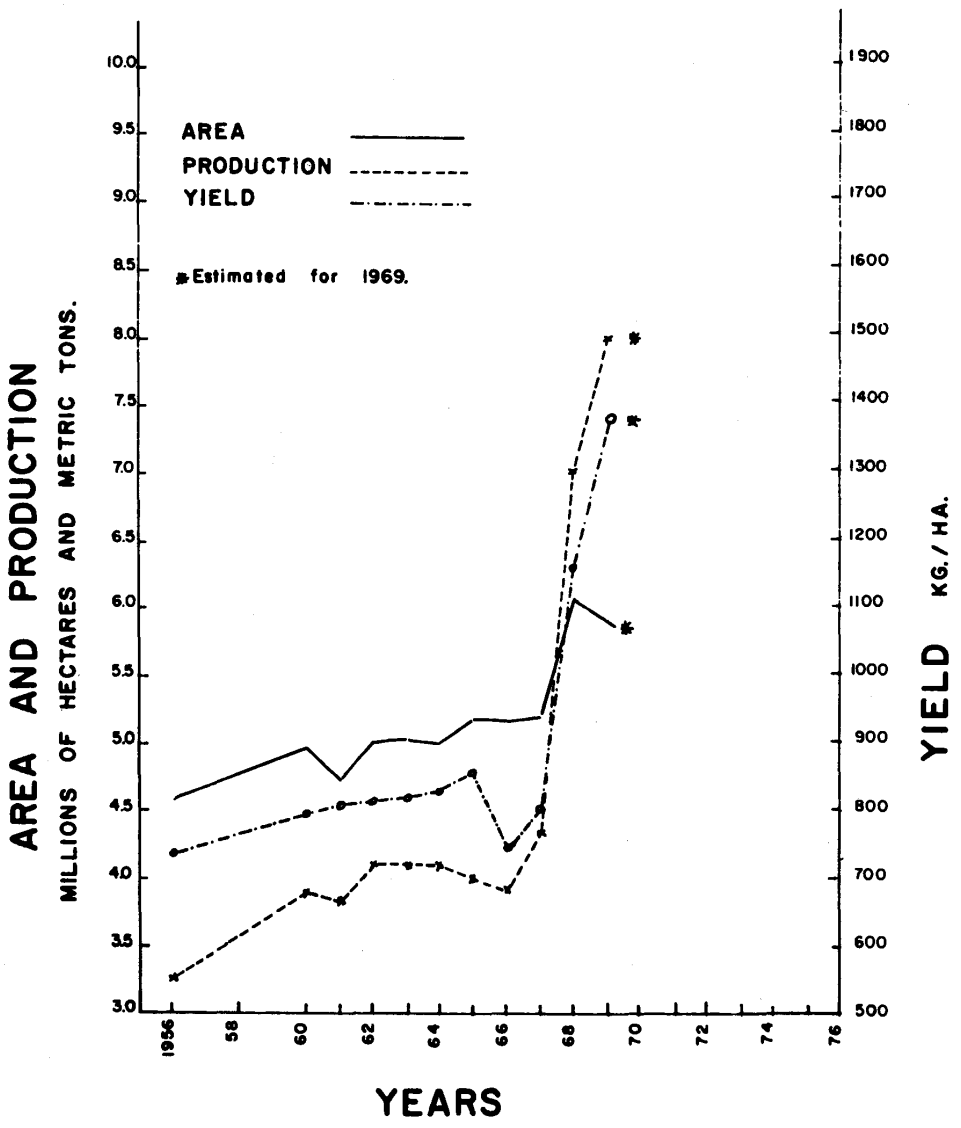


Figure 4. Cultivated area, production and yield of wheat in West Pakistan.

Rather we should be visionary and imaginative in our plant breeding programs if we hope to stay ahead of demands for food, feed, wood, and fiber. To accomplish this we must use every new approach that seems feasible, not only to improve the current crop species but also to create entirely new crop or tree species through the use of wide crosses. To illustrate my point, I would like to briefly outline our experiences on Triticale breeding during the past 4 years.

TRITICALE. THE FIRST MAN-MADE SPECIES THAT SHOWS PROMISE OF BECOMING A MAJOR CEREAL CROP

Triticales are amphiploid derivatives of a cross between wheat and rye. When such a cross is made, the hybrid seed produced gives rise to a completely sterile plant. If, however, the seedling arising from the hybrid F_1 seed is suitably treated with colchicine, the chromosomes of both the wheat and rye components of the hybrid seedling are doubled. This results in a seedling which develops into a partially fertile plant that produces seed.

Triticales have been known since 1888. However, until about 40 years ago, they were mostly academic curiosities. During the past three decades several scientists, especially Muntzing in Sweden and Sanchez-Monge in Spain, have devoted most of their professional careers to the improvement of this artificial species. In 1964 CIMMYT in collaboration with the University of Manitoba began a breeding program designed to develop Triticale varieties that would be competitive with wheat, barley, rye, and oats.

Until about 1-1/2 years ago the development of Triticales had been stymied by two main obstacles, partial sterility and shrivelled grain. In April 1967, Drs. Frank J. Zillinsky and George Varughese of our staff discovered 7 F_3 plants that were highly fertile. These subsequently have been reselected and resown 5 times under 4 widely different climatic conditions. They have remained highly fertile in all plantings. We also have crossed the fertile types to sterile and partially sterile types and have found that the first generation progeny are fertile, thus indicating that this character is heritable. During the past year we have isolated some types that have far better grain types than those that were previously available. In our program we have also developed dwarf early-maturing, daylength-insensitive lines and some types which are highly resistant to diseases. At the present time we are combining these various desirable characters, through further crossing. I am now completely convinced that Triticale varieties will be developed within the next 8 years that will be competitive, yield-wise, with the best wheat, oats, and barley varieties.

On the basis of the breakthrough in overcoming sterility, combined with very considerable improvement in grain plumpness, we have now greatly expanded our Triticale breeding program. The progress reported above has been achieved in the hexaploid Triticale types, those derived from crossing *Triticum durum* Desf. wheat with rye. We are making many new Triticales at this ploidy level involving many different durum wheat varieties and different rye varieties. We are also now making many new octaploid Triticales, derived from crossing bread wheat varieties (*T. vulgare* Vill.) with rye. We visualize developing Triticales both as a food and a feed grain. Preliminary research indicates that it should be possible to develop varieties with high levels of both lysine and total protein, which would enhance their value nutritionally (Borlaug, in press).

We in CIMMYT are now convinced that Triticale - a man-made cereal species - is on the verge of becoming a commercial crop that will compete successfully with other small grains. How soon this happens will depend largely upon the amount of research effort that is devoted to further improving this species. CIMMYT is distributing its best lines to all research organizations who are interested in working with this new crop.

WHAT ARE THE POSSIBILITIES OF DEVELOPING OTHER MAN-MADE CROPS OR TREE SPECIES?

The rapid progress now being made in the improvement of Triticales naturally stimulates one to consider the feasibility of making other wide crosses, either for the improvement of parent crop plants or for the creation of entirely new ones.

Within the past decade, as has been indicated by Dr. Ernst Schreiner, tremendous progress has been made in the basic sciences that bear on the feasibility of such undertakings. It is now possible to grow haploid plants of rice, barley, and wheat from anthers, when the proper media are employed (Nichell and Torrey, 1969). Embryo culture techniques have improved greatly. Tissue culture techniques, involving the use of hormones and many new, more efficient nutrient media, have produced spectacular results. It is now possible to isolate apparently undamaged individual protoplasts of wheat, carrot, tomato, soybeans, and other species by the use of the enzymes pectinase and cellulase. In some cases when cellulase has been removed from the system, the protoplasts have been able to resynthesize the cell wall. Fusions also have been obtained between two protoplasts within a species.

These events definitely open the door to the possibilities of using protoplasmic fusion and cell hybridization as a future tool in plant breeding. It is now possible, employing proper techniques, to begin with a single somatic tissue cell of many different plants, i.e., carrot, tobacco, endive, parsely, rice, and sugarcane, and regenerate the entire plant, including the production of seed. Hybrid seed and seedlings have been obtained from wide crosses by using Giberellic acid to facilitate the consummation of fertilization, followed by embryo culture. Using such techniques, Kruse has reported obtaining hybrid seedlings of *Hordeum* x *Secale* and more recently, tentatively, between *Avena* x *Triticum* (personal communication). To date, however, there has been no report of his having formed the amphidiploid of these hybrids.

Although I am fascinated by the eventual feasibility of using cell hybridization for plant improvement, I nevertheless feel that there are other avenues that are more immediately feasible. In light of our recent success in progress with Triticale improvement, and Dr. A. Kruse's preliminary report on successful hybridization of barley x rye, and oats x wheat, and the reported but unproven occurrences of natural hybrid seedlings of maize and sorghum, it now appears the time has come to launch an aggressive program in crop plant improvement based on wide crosses. I propose that such a program be undertaken to improve both cereals and legumes. It should include attempting to make as many crosses between different genera of cereals as possible, employing all of the most modern techniques to consummate fertilization, to cultivate the embryoes, and to form the amphidiploids. If a series of amphidiploids of diverse genetic backgrounds can be produced, this will open the door to vast further improvement through conventional breeding approaches. I feel

that the time has come to undertake a major attempt to improve our crop plants or to create entirely new ones through this type of approach. I believe that one or more of the International Research Institutes can be an effective catalyst in exploring the feasibility of such an approach to plant breeding.

I personally want to live to see what happens when the amphidiploid is produced between wheat and rice. Since rice is the only small grain cereal that does not have its corresponding rust or rusts (*Puccinia* spp.), will it confer its immunity to the wheat x rice amphidiploid? Or will man by such scientific folly open a Pandora's box and form a bridging species which would open the floodgates to invasion of rice by the wheat disease parasites and vice-versa? Were this to happen, we would have set the stage for the "Death of Grass" as envisioned by novelist John Christopher.

In the face of the continuing, relentless pressure of population growth, I believe it is absolutely necessary for plant and tree breeders to use more and more imagination and aggressiveness to produce higher yielding plants, and thereby hold the line on the food and fiber production front. By so doing, agriculturists and foresters can buy an additional 2 or 3 decades in the hope that by then *Homo sapiens* will wake up to the pending cataclysm of continued, uncontrolled population growth. Social, biological (human) Utopia is a goal we should strive to achieve, but as biologists (and especially as geneticists) we know that at best it can be only a working hypothesis. We must channel, guide and cultivate our idealism wisely if we are to improve the living standards of the world's masses, and if we are to survive as a species. Unbridled idealism and emotionalism, unguided by reason and common sense, can unfortunately also lead us into oblivion.

To the ecologists and environmentalists, who are feverishly working to prevent further deterioration of our environment and who are now finally being heard and getting a "big play" in television, radio and the press, I say, beware of conveying an oversimplified, distorted picture of achieving a rapid and permanent solution to this problem, for you are dealing with only one isolated aspect of the larger, complex population problem. To the millions of idealistic students who are actively, and vociferously, concerned with changing governments and building a better world where peace will reign and where the rights of all individuals will be given complete expression, I say, beware of being misled into believing that any kind of government - capitalistic, socialistic, communistic, anarchistic or military dictatorship - can provide such a Utopia while essentially ignoring the underlying, monstrous, and evergrowing human population problem. We only need to reflect on the degenerative social behavior of rats in overpopulated cages; or on the periodic suicidal migrations of the Arctic lemming, which springs from response to overcrowding and is led by the younger members of the population, to know that we must face up to the population growth problems if we are to survive. The time is late!

Although I have built the last part of this presentation around a plea for more creative breeding in food crops, I also now challenge all forest geneticists and tree breeders "to think big --- think and act Paul Bunyan!"

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WORKING PARTY REPORT VI

INTERNATIONAL UNION OF FOREST RESEARCH ORGANIZATIONS INTERSECTIONAL WORKING GROUP ON GENETIC RESISTANCE TO FOREST DISEASES AND INSECTS

Richard T. Bingham, Howard B. Kriebel, and J. Gremmen
REPORT OF THE 1969 ORGANIZATIONAL MEETINGS OF THE COMMITTEE ON WHITE PINE BLISTER RUST 645

REPORT OF THE 1969 ORGANIZATIONAL MEETINGS of the COMMITTEE ON WHITE PINE BLISTER RUST of the INTERSECTIONAL WORKING GROUP ON GENETIC RESISTANCE TO FOREST DISEASES AND INSECTS of IUFRO SECTIONS 22 (STUDY OF FOREST PLANTS) AND 24 (FOREST PROTECTION)

by

R. T. Bingham, Chairman, Committee on White Pine Blister Rust
H. B. Kriebel, Chairman, Subcommittee on Procurement and Exchange of Breeding Materials
J. Gremmen, Chairman, Subcommittee on International Resistance Test Facilities

BACKGROUND INFORMATION AND COMMITTEE OBJECTIVES

The First FAO World Consultation on Forest Genetics and Tree Improvement, meeting in Stockholm in August, 1963, recognized the need for coordination of the work of forest geneticists, pathologists, entomologists, and physiologists in securing pest-resistant trees, and recommended that the International Union of Forest Research Organizations (IUFRO) establish a "Working Group on Parasite Resistance." In response to this recommendation, at the 14th IUFRO Congress in Munich, September, 1967, IUFRO Section 22 (Study of Forest Plants--J. D. Matthews then leader) and Section 24 (Forest Protection--A. Biraghi then leader) established an Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects, appointing H. D. Gerhold of the U.S.A. as Working Group Chairman. Then during late 1967 and 1968 Dr. Gerhold established six disease and insect resistance committees within the Working Group, appointing R. T. Bingham as Chairman of a Committee on White Pine Blister Rust.

Thus the Committee on (resistance to) White Pine Blister Rust became functional about 1-1/2 years ago. Initially the Chairman, working with a small group of volunteer committee members (P. Schütt, Germany; R. F. Patton, U.S.A.; B. F. Søegaard, Denmark) set about the business of determining committee objectives, establishing a committee to attain these objectives, and planning an organizational meeting.

First, questions of pertinent committee objectives were explored. One thorny question was paramount. Was securing lasting genetic resistance to the white pine blister rust disease mainly a North American problem, a North American and north European problem, or was it truly a world-wide problem?

With the inadequacy of forest genetics-pathology-physiology funds; with the successful replacement of once-favored but blister-rust-eliminated white pine introductions in northern Europe by Douglas-fir, other pines, spruce, etc.; with the presence of highly resistant native white pines in mainland Asia; with the absence of the rust and no present threat to susceptible native and exotic white pine species in Japan; and with major, commercial white pine resources of the world now concentrated in North America; by necessity (not by default) the problem became identified as North American. However, recognizing the great promise that *Pinus strobus* and other introduced white pines held for north European and to a lesser extent Asian forestry, research and forest management administrators of these continents expressed general interest in utilizing resistant white pines, once developed. However, with replacement of rust-decimated white pines with other productive and less-troublesome species, and with their limited research and management finances thus channeled toward the more pest-free species, administrators were reluctant to invest in further local research and testing toward securing white pine blister rust resistance.

Unfortunately, the problem of developing blister rust resistant white pines for north European and Asian forestry is not one that can be solved entirely in North America. Ultimately, because resistant types developed in North America may be exposed to new and different races of the rust fungus in Europe and Asia, the problem again takes on international aspects. One might say with this possibility of rust race differences the problem becomes even more difficult and costly. In so doing, however, he discounts progress toward lasting resistance made by the cereal crop breeders, and by the horticulturists, as well as the existence of balanced or endemic host:pathogen systems in many tree:rust associations. He also discounts his ability to employ developed technology in securing lasting resistance in his particular local environment.

It is true that North American white pine blister rust resistance programs will benefit through exposure of their resistant types to a probably greater number of pathogenic races of the white pine blister rust present nearer the Eurasian gene-centers of the rust. But if long-range needs for restoring white pines to European and Asian forestry are great enough, then forestry in these continents will also benefit by development of a broad-spectrum, lasting resistance for worldwide use.

The decision is really one of how much longer foresters can permit themselves to take the short-term view on forest pest problems. Seemingly vast resources in relatively pest-free endemic and introduced species are not inexhaustible. There is no important tree species, however pest-free now, that is any more immortal than the white pines. All are seriously threatened by as yet unintroduced but internationally dangerous tree pests (for instance European and Asian hard pines known to be highly susceptible to a variety of North American tree rusts). Can we much longer abandon key species, native or introduced, one by one? Alternatively, for securing the maximum productivity of forest lands--a goal which all foresters recognize as highly important in the face of a growing world population--should we not be bolstering resistance in each problem species so as to have replacement species at hand when the next decimating pest eliminates another key species for a rotation or two?

Facing these facts, the Committee decided that work toward international restoration of white pines might be technically and financially difficult, but that in the long run the work of restoration should be

undertaken, definitely and aggressively. This became the major objective of the Committee. Initial emphasis was to be directed toward restoration of commercially important white pines for medium and high-hazard rust areas. Attention was also to be directed toward those white pine species important to watersheds and wildlife, as well as toward those of great aesthetic and ornamental value.

Next, an 18-man committee embodying wide coverage of the world's white pine species was assembled.

Finally, the time and place of the Advanced Study Institute on Biology and International Aspects of Rust Resistance in Forest Trees, set for August 1969, at the University of Idaho, Moscow, Idaho, U.S.A., was chosen as a particularly advantageous time and place to hold first, organizational meetings of the Committee.

The report on Committee and Subcommittee organization, meeting preparations, meeting action, and Subcommittee recommendations follows:

COMMITTEE ORGANIZATION

As mentioned above Chairman Bingham was appointed by Working Group Chairman Gerhold in late 1967. Bingham, working with a volunteer nucleus of Committee members, then established two Subcommittees; (1) a Subcommittee on Procurement and Exchange of (white pine) Breeding Materials,[1] H. B. Kriebel, U.S.A., Chairman, and (2) a Subcommittee on International (white pine blister rust) Resistance Test Facilities, J. Gremmen, Netherlands, Chairman. Then, working with the two subcommittee chairmen additional Committee Members, each with special qualifications for performing subcommittee functions, were appointed. Present Committee staffing is as shown below; additional members may be added as needed.

A. Committee Chairman

R. T. BINGHAM, U.S. Dep. of Agriculture, Forest Service, Intermountain Forest & Range Exp. Sta., Forestry Sciences Laboratory, P.O. Box 469, Moscow, Idaho 83843, U.S.A.

B. Subcommittee on Procurement and Exchange of Breeding Materials

[1] *Editor's note: Later in 1969, R. Z. Callaham, Leader of IUFRO Section 22, with the concurrence of E. Björkman, Leader IUFRO Section 24, H. D. Gerhold, Chairman of the Intersectional Working Group, R. T. Bingham and H. B. Kriebel, elevated the Subcommittee on Procurement and Exchange of (white pine) Breeding Materials to full Section 22 Committee status, as a new IUFRO Section 22 Committee on Breeding of White Pines. Here, as well as serving needs of the White Pine Blister Rust Committee of Dr. Gerhold's Intersectional Working Group on Genetic Resistance of Forest Insects and Diseases, the new Committee will also serve white pine seed, pollen and other needs of 3 other IUFRO Section 22 Working Groups. These are the Working Groups on (1) International Provenance Trials, P. Bouvarel, Chairman, (2) Procurement of Seed for Provenance Research, H. Barner, Chairman, and (3) Hybridization among Species and Provenances, A. deJamblinne, Chairman.*

Subcommittee Chairman

H. B. KRIEBEL, Forestry Dep., Ohio Agricultural Research and Development Center, Wooster, Ohio 44691, U.S.A., coordinating coverage of U.S.A. and Central American white pines.

Subcommittee Members

J. A. AHSAN, Pakistan Forest Institute, P.O. Forest Institute, Peshawar, WEST PAKISTAN, covering West Pakistanian, Afghanistanian, and possibly Jammu and Kashmir *P. wallichiana*.

V. BENEA, Institutul de Cercetari Forestiere, Bucharest, *RUMANIA* (now c/o School of Forest Resources, North Carolina State University, Raleigh, N.C. 27607, U.S.A.), covering *Pinus cembra* in Rumania and the eastern Ukraine.

P. D. DOGRA, Tree Genetics Laboratory, National Botanic Gardens, Lucknow, INDIA, covering *P. wallichiana* (*P. griffithii*) in India.

C. C. HEIMBURGER, retired, Research Branch, Ontario Dep. of Lands and Forests, 80 Haddington Avenue, Toronto 380, Ontario, CANADA, covering Canadian *P. strobus*, *P. monticola*, *P. albicaulis*, and *P. flexilis*.

M. HOLUBCIK, Vsykumny ustav lesneho hospodarstva, Strakonicka cesta, Zvolen, CZECHOSLOVAKIA, covering *P. cembra* in Czechoslovakia.

K. HOLZER, Forstliche Bundesversuchsanstalt, Institut für Forstpflanzenzüchtung und Genetik, A 1147, Wien-Mariabrunn, AUSTRIA, covering Austrian *P. cembra*.

S. K. HYUN, Institute of Forest Genetics, Suwon, Kyunggido, KOREA, covering Korean *P. koraiensis*, *P. pumila*, and *P. parviflora* (*P. pentaphylla* var. *himekomatsu*), and Taiwan *P. armandii*.

B. NICOTA, Sumarski Institut, Engelsova 2, Skopje, YUGOSLAVIA, covering Yugoslavian and possibly Albanian and Grecian *P. peuce*.

H. SAHO, Laboratory of Forest Botany, Faculty of Agriculture, University of Tokyo, Bunkyo-ku, Tokyo, JAPAN, covering Japanese *P. parviflora* (*P. pentaphylla* and *P. pentaphylla* var. *himekomatsu*), *P. koraiensis*, *P. pumila*, and *P. armandii* var. *amamiana*

D. VELKOFF, Academie des Sciences Agricoles de Bulgarie, Institut des Forests, Sofia-Simeonovo, BULGARIA, covering Bulgarian *P. peuce*.

(No coverage is as yet provided for Chinese mainland *P. armandii*, *P. koraiensis*, *P. sibirica*, *P. pumila*, *P. wallichiana*, *P. fenzeliana*, and *P. wangii*; for Vietnamese *P. dalatensis*; for Tibetian *P. armandii* and *P. wallichiana*; for Taiwanese *P. morrisonicola*; and for U.S.S.R. *P. sibirica*, *P. pumila*, and *P. koraiensis*.)

C. Subcommittee on International Resistance Testing Facilities

(All members represent countries where the white pine blister rust hazard is present and high, and where there is some desire to restore or supplement white pine forests.)

Subcommittee Chairman

J. GREMMEN, Section of Pathology and Resistance Research, Stichting Bosbouwproefstation "De Dorschkamp", Bosrandweg 20, Postbus 23, Wageningen, NETHERLANDS.

Subcommittee Members

B. K. BAKSHI, Forest Pathology Branch, Forest Research Institute and Colleges, P.O. New Forest, Dehra Dun, INDIA.

R. J. HOFF, U.S. Dep. of Agriculture, Forest Service, Intermountain Forest & Range Exp. Sta., Forestry Sciences Laboratory, P.O. Box 469, Moscow, Idaho 83843, U.S.A.

R. F. PATTON, Dep. of Plant Pathology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

P. SCHÜTT, Forstbotaniches Institut, Universität München, 8000 München 13, Amalienstrasse 52, GERMANY.

B. F. SØEGAARD, Royal Veterinary and Agriculture College, Arboretet, Hørsholm, DENMARK.

L. ZUFA, Research Branch, Ontario Dep. of Lands and Forests, Maple, Ontario, CANADA.

ORGANIZATIONAL MEETING PREPARATIONS

After staffing of the Committee and Subcommittees, Chairman Bingham suggested that three general problems were in need of consideration by the whole Committee, because these might slow progress at the organizational meeting and hinder future Committee operations. These problems were (1) the lack of uniformity in usage of white pine taxonomy, leading to confusion as to the identity and general or specific source-locality of white pine materials, (2) the scarcity of critical information on relative blister rust resistance of white pine species, and (3) the confusion and insufficiency of information on the origin (or possible gene-centers) of *Cronartium ribicola*. A 4-page memorandum outlining these problems and the action needed upon them was circulated to all Committee Members July 14, 1969.

Subcommittee Chairman Kriebel also circulated a memorandum to members of the Subcommittee on Procurement and Exchange of (white pine) Breeding Materials on June 2, 1969, requesting consideration and advice on 12 items of potential Subcommittee business including (1) white pine species to be considered, (2) types of material for exchange, (3) types of trees to be used for collection, (4) methods of stand location, (5) selection of sampling locality, (6) collection timing, (7) collection supervision, (8) number of trees per provenance and seeds per tree, (9) financing of collections, (10) coordination of collection work, (11) plant

quarantine problems and (12) record keeping on collection locality and seed disbursal.

Similarly, Subcommittee Chairman John Gremmen circulated a memorandum July 28, 1969, to members of the Subcommittee on International (blister rust) Resistance Testing Facilities, requesting information on (1) the sort of facilities needed, (2) where they should be established, and (3) how they should be operated and financed. Also, with the assistance of subcommittee member B. F. Søegaard, on February 27, 1969, Chairman Gremmen circularized about 50 European forestry agencies--those conceivably interested in restoring white pines for general forestry use in their countries--requesting information on their interest and possible cooperation in international research on blister rust resistance.

COMMITTEE AND SUBCOMMITTEE ORGANIZATIONAL MEETINGS AUGUST 18-23, 1969

A. General Committee Meeting

The Committee on White Pine Blister Rust met in general session August 18, 1969, in Conference Room 1, of the University of Idaho, Wallace Residence Center, Moscow, Idaho, U.S.A.

Present were Committee Chairman Bingham; Subcommittee Chairman Kriebel and Subcommittee on Procurement and Exchange of Breeding Materials Members Heimburger, Holzer, Hyun, Saho, Nicota, and Ahsan (the latter two members as represented by M. Vidakovic); and Subcommittee Chairman Gremmen, and Subcommittee on International Resistance Test Facilities Members Hoff, Patton, Schütt, Søegaard, Zufa, and Bakshi (as represented by S. Kedharnath). Also present was H. D. Gerhold, Chairman of the parent IUFRO Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects, and visitors, R. J. Steinhoff, B. B. Kinloch, A. Klingström, F. Cech, K. von Weissenberg, plus others not recorded.

Five general items of business were disposed of, as follows:

(1) White Pine Taxonomy. There was general agreement that the white pine taxonomy as presented in Critchfield, William B., and Elbert L. Little, Jr., Geographic Distribution of the Pines of the World. U.S. Dep. Agr., Forest Service, Misc. Publ. 991. 97 pp. Feb., 1966, should be used in all future communcations between Committee Members. It was recommended, however, that the species *Pinus griffithii* McClell., up for reconsideration and rejection in favor of *P. wallichiana* A.B. Jackson (by the Standing Committee on Stabilization of the International Association for Plant Taxonomy) for the time being always be given in conjunction with its synonym *P. wallichiana* A.B. Jacks.

It was also recommended that the Japanese *P. parviflora* complex be further investigated by the appropriate Committees of the International Association for Plant Taxonomy, toward more clearly defining the taxons of the complex variously known as *P. pentaphylla* Mayr (for the northern taxon of S. Hokkaido and central to northern Honshu) and *P. pentaphylla* Mayr var. *himekomatsu* Makino or *P. himekomatsu* Miyabe and Kudo (for the southern taxon of central and S. central Honshu). A Committee recommendation to this effect was prepared by Hoff and Vidakovic, and this recommendation has since been handcarried by Kriebel to the appropriate

taxonomical Committees at the 11th International Botanical Congress, that convened August 25-29 in Seattle, Washington.[2]

Dr. E. L. Little, Jr., kindly sent sufficient copies of the Critchfield and Little paper so that each Committee member could have a personal copy.

The accepted white pine taxonomy, with notes on synonomy, common names, botanical ranges and crossability of species is also given in Bingham's first article in these proceedings.

(2) The question of gene-centers for *Cronartium ribicola*, i.e., one in Asia, and another in the European Alps possibly separated in the Pleistocene by Eurasian glaciation, was discussed by Subcommittee Chairman Gremmen. However, presently coverage of the literature and herbaria remains scanty, so the question was tabled in view of John Gremmen's volunteering to investigate the matter further and report on it again at a later date (possibly at the Gainesville, Floria, IUFRO meetings in March 1971).

(3) The question of securing more meaningful white pine blister rust resistance ratings for the world's white pines was discussed with the opinion emerging that really sound ratings will have to await provision of a much wider range of materials by Kriebel's Subcommittee, and a more thorough, worldwide testing thereof. Meanwhile, Bingham's incomplete, tentative rankings (first article, these proceedings) will serve.

(4) Bingham, Zufa, and Patton agreed that Committee Members and other cooperators should have complete access and use of materials already sent elsewhere in the world by the three white pine blister rust resistance programs carried on by the U.S. Forest Service, Intermountain Forest and Range Experiment Station, the Ontario Department of Lands and Forests, and the University of Wisconsin Department of Plant Pathology, at the discretion of the testing agency. It was noted that exact data on origin and value of the material should be sought using the originator's plant material numbers.

(5) A newly introduced item of business was also discussed and acted upon. This concerned the preservation of better stands of two white pine species or varieties, apparently being threatneed by conversion of natural stands to other faster-growing conifers. The first of these species was *Pinus armandii* in Taiwan, the second the central and southern Honshu taxon of Japanese *P. parviflora* (i.e., *P. pentaphylla* var. *himekomatsu*, or *P. himekomatsu*). Because these germ plasm sources, especially the better stands thereof, are likely to be valuable in breeding for white pine blister rust resistance and for other purposes, Chairman Bingham was directed to prepare brief recommendations to the Governmental and other agencies concerned, asking for preservation of at least a few better stands of each taxon. S. K. Hyun prepared a skeleton recommendation and provided addresses of Taiwanese officials to be contacted in respect to *P. armandii*, and H. Saho prepared and provided similar materials for the central Honshu taxon of *P. parviflora*. The Chairman will now contact agencies involved to determine what, if any, steps are now contemplated to preserve better stands of the two taxa and the extent of original and

[2] *Editor's note: It is now (January 1971) known that the Standing Committee on Stabilization did not act on the Committee on White Pine Blister Rust recommendation during the Seattle Botanical Congress. However, action is imminent, teste Dr. E. L. Little, Jr.*

remaining stands. Then, through H. D. Gerhold, Chairman of the parent Working Group, he will contact the land managing agencies concerned and the International Union for the Conservation of Nature, with a concrete proposal for preservation of select stands.[3]

General discussion on these five general business items and on proposed action thereon was invited by participants at the Advanced Study Institute, then in session, at open meetings on Wednesday, August 20 and Saturday, August 23, 1969. The proposed actions received general approval.

B. Subcommittee Meetings

The two Subcommittees met on successive evenings August 18 and 19, 1969, to discuss operational problems and to prepare recommendations. John Gremmen's Subcommittee also met for an hour the morning of August 23. Recommendations are given below.

Those of the Subcommittee on Procurement and Exchange of (white pine) Breeding Materials submitted by H. B. Kriebel are quite lengthy and detailed. This is because they serve as a preamble for recommendations of both Subcommittees--tying the work of the Subcommittees together and detailing the Committee's concern with securing materials for provenance as well as for resistance testing. Those of the Subcommittee on International (white pine blister rust) Resistance Testing Facilities may, in contrast, appear to be quite short and general. This reflects the presently scanty information available to the latter Subcommittee concerning (1) potential N. European and Asian cooperators and test sites, (2) exact amounts of white pine species materials that will become available for resistance testing through Kriebel's Subcommittee, (3) exact amounts and quality of tested, improved materials of *P. strobus, P. monticola, P. lambertiana, P. peuce,* etc., available, (4) suitable and economical experimental designs for testing species or improved materials, (5) extent and timing of examination schedules for these tests, and (6) means for financing the tests. Action to relieve these informational voids is indicated in the recommendations or discussion that follows them.

1. *Recommendations of the Subcommittee on Procurement and Exchange of Breeding Materials*, of the IUFRO White Pine Blister Rust Committee

The gene pool available for white pine breeding includes a number of other species besides *Pinus strobus* and *Pinus monticola*. Since there is evidence of genetic resistance to white pine blister rust in several of these species, there is a need for procurement and exchange of these potentially valuable breeding materials. There is also a considerable interest in the use of these species for breeding objectives other than rust resistance.

[3] *Editor's note: The Chairman of the Committee on White Pine Blister Rust did so act, on September 16 and 17, 1969, initiating inquiries in respect to preservation of representative natural stands of* Pinus armandii *and* P. morrisonicola *in Taiwan, or of* Pinus pentaphylla *and* P. himekomatsu *in Japan. So far, efforts toward preservation of the two Taiwanese species are well along toward preservation of several specimen stands of* P. armandii *and* P. morrisonicola. *Those aimed at preserving Japanese white pines, however, have not progressed beyond the initial inquiry.*

Therefore, the Subcommittee on Procurement and Exchange of (white pine) Breeding Materials makes the following recommendations:

(1) That it be authorized by the Working Group Chairman to canvass research institutions throughout the world concerned with white pine breeding for blister rust resistance, to determine their requirements for seed;

(2) That the seed survey be extended to institutions engaged in white pine breeding for objectives other than rust resistance, in order to extend the work to all white pine species, avoid duplication of effort, and provide for coordination and cooperation;

(3) That seed collections be made from indigenous stands, selected insofar as possible to provide a representative sampling of the gene pool of the species;

(4) That special attention be given to *Pinus griffithii* (syn. *P. wallichiana*) because of its importance in breeding programs for both rust resistance and increased yield. (It is anticipated that tests of this species will be large-scale, because of the probable wide variation within the species.)

(5) That in view of the world-wide interest in *Pinus strobus*, consideration be given to procurement and exchange of breeding material of this species, recognizing that in many areas a prerequisite may be the establishment of blister rust test facilities and a special program for the selection of potentially rust-resistant trees, rather than a mass selection program;

(6) That other species of white pines should be included in the procurement and exchange program, insofar as possible. (Species of interest are *Pinus monticola, Pinus peuce, Pinus koraiensis, Pinus armandii, Pinus strobiformis, Pinus parviflora* (synonyms *Pinus pentaphylla* and *Pinus himekomatsu*), *Pinus lambertiana, Pinus cembra, Pinus sibirica, Pinus albicaulis, Pinus flexilis, Pinus aristata,* and *Pinus balfouriana*);

(7) That financing or barter arrangements be established for each species as needed, the method possibly being different for different species or groups of species (i.e., undertaken by scientist-to-scientist or institute-to-institute cooperation, by subscription, by a foundation, by a governmental agency, or by a combination of these methods);

(8) That procurement arrangements for *Pinus griffithii* begin as soon as possible after a collection plan is developed, with an effort to obtain seed collections by the autumn of 1971, and that similar efforts be made as soon as possible on *Pinus peuce, Pinus koraiensis,* and *Pinus armandii*;

(9) That the Subcommittee on Procurement and Exchange of Breeding Materials be authorized to provide the leadership in the planning and organization of these collections and exchanges, working when desirable through other agencies and programs, and, through its Chairman, maintaining close contact with such agencies; and finally,

(10) That close liaison be maintained with IUFRO's Working Group on International Provenance Testing (P. Bouravel, Chairman) and with its Working Group on the Procurement of Seed for Provenance Tests (H. Barner,

Chairman), since a part of the procurement effort will be directed toward the provenance testing objective of the former Working Group, and because of the possibility that white pine seed procurement might be arranged through the latter Working Group.

Submitted by--
Howard B. Kriebel, Chairman
C. Heimburger
K. Holzer
S. K. Hyun
M. Vidakovic (for B. Nicota and J. A. Ahsan)
H. Saho

These procurement and exchange recommendations were also discussed in open committee sessions August 20 and 23, 1969, and participants at the Advanced Study Institute were there invited to comment and suggest improvements or additions to the recommendations. In respect to recommendation (1), Chairman H. D. Gerhold of the Intersectional Working Group on Genetic Resistance to Forest Diseases and Insects, being present gave immediate approval for canvassing research institutions. In respect to all 10 recommendations, general approval was obtained from the Study Institute participants, from two other IUFRO Section 22 Working Group Chairmen present (K. Stern and A. de Jamblinne), and from Section 22 Chairman R. Z. Callaham, also present.

2. *Recommendations of the Subcommittee on International Resistance Test Facilities*, of the IUFRO White PIne Blister Rust Committee

The Subcommittee "International Resistance Test Facilities" makes the following recommendations:

(1) That the Subcommittee, through its Chairman, will make inquiries to find which institutions are willing to cooperate in the white pine blister rust testing program, and

(2) That the Subcommittee, after assembling basic information, will investigate the possibilities for the establishment of disease gardens in various countries with the aims of investigating the existence of other physiological races and searching for additional resistance against the blister rust fungus.

Submitted by--
J. Gremmen, Chairman
S. Kedharnath (for B. K. Bakshi)
R. J. Hoff
R. F. Patton
P. Schütt
B. F. Søegaard
L. Zufa

Concerning these two recommendations, there is much discussion and proposed Subcommittee activity that should be reported. In the Subcommittee meeting of August 23, it was agreed that the Subcommittee Chairman would circulate two separate inquiries to potential cooperators in the medium to high blister rust hazard areas of Europe (including Scandinavia and Great Britain), India-Pakistan, and North America.

The first of these inquiries, to be circulated immediately to cooperators in all three continents, would be restricted to the testing of unimproved materials of any and all white pine species as supplied by Kriebel's subcommittee. Generally these would be tested, in large or small tests, at the cooperator's discretion and expense. These "species trials" would be aimed at giving cooperators a greater opportunity to appraise or reappraise white pines perhaps already useful for immediate introduction, and at building a more meaningful and internationally useful white pine species resistance rating. This work should have general interest in all hazard-zone countries, since only fragmentary work has been undertaken to appraise resistant species (*P. griffithii, P. peuce, P. armandii, P. koraiensis, P. sibirica,* etc.) for immediate introduction, or to appraise use of these promising species in hybridization work for improvement of resistance in native species.

The second of these inquiries would be aimed only at potential cooperators in high-hazard countries of northern Europe and Asia, and would be concerned with the much more detailed and expensive testing of improved *P. strobus, P. monticola, P. lambertiana,* and possibly *P. peuce* varieties of demonstrated resistance where tested in the U.S.A. and Canada. This second inquiry will be some time in preparation. The Subcommittee agreed that an "Ad Hoc Panel of Experts" (Hoff, Patton, and Zufa, also seeking advice and information on resistant materials from Washington-Oregon, California, and Lake States resistance programs) would assemble necessary information to supplement the inquiry. Included would be (1) information on location and availability of specified materials embodying demonstrated resistance, and (2) where possible, specific information on the host: parasite reactions and resistance genes involved in the resistance reactions of the improved material; also recommendations on (3) suitable experimental designs, (4) spacing and numbers of seedlings and families to be tested, (5) methods of exposure to the rust, (6) examination items and timing, and (7) other treatments of seed or seedlings necessary to insure establishment of a suitable test for evaluation of resistance under exposure to possibly new and different races of the rust fungus.

Hopefully the Ad Hoc Panel will provide this information to Subcommittee Chairman Gremmen within 12 months, allowing him to circulate the second inquiry and receive responsive answers within 12 to 18 months.

These recommendations and action plans were also discussed and given general approval by the IUFRO representatives and Advanced Study Institute participants at the open meetings August 20 and 23, 1969.

In closing this report, the Chairman of the White Pine Blister Rust Committee would like to thank the present Leaders of IUFRO Sections 22 and 24 (R. Z. Callaham and E. Björkman), the Chairman (H. D. Gerhold) of the Intersectional Working Group, Subcommittee Chairmen H. B. Kriebel and J. Gremmen, and the other 16 members of the White Pine Blister Rust Committee for their staunch and untiring support, for their valuable contributions to Committee work, and for their equally valuable contributions to the Advanced Study Institute. The chairman would also like to acknowledge, with warm thanks, the contributions of other participants of the Advanced Study Institute given at open committee sessions August 20 and 23.

I feel that the Committee is off to a good start, and that much of the credit for this goes to the many scientists and tree breeders who helped us with our problems at this initial meeting. All of us on the Committee will now aim toward reporting significant progress at the 15th IUFRO Congress, in Gainesville, Florida, March 1971.

Respectfully submitted,

R. T. BINGHAM
Chairman of the
White Pine Blister Rust Committee

August 29, 1969, Moscow, Idaho, U.S.A.

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