



*Possibilities of Breeding
Weevil-Resistant
White Pine Strains*

by

*Jonathan W. Wright
William J. Gabriel*



STATION PAPER NO. 115 • NORTHEASTERN FOREST EXPERIMENT STATION • 1959
FOREST SERVICE • U.S. DEPARTMENT OF AGRICULTURE • UPPER DARBY, PA.
RALPH W. MARQUIS, DIRECTOR

Acknowledgments

THESE studies were made while the authors were stationed at the Morris Arboretum, Philadelphia, Pa., where some of the forest genetics work of the Northeastern Station is conducted in cooperation with the University of Pennsylvania.

Grateful acknowledgment is made to the Arboretum staff for the liberal use of their plant material and for their helpful encouragement.

We are particularly indebted to the workers at the Forest Insect and Disease Laboratory of the Northeastern Forest Experiment Station, New Haven, Conn., for their help in locating stands suitable for study and for information on the ecology of the insect.

Many of the observations were made on plantations established by the Conservation Department of the State of New York. Their excellent system of records, which gives the seed origin, planting date, subsequent treatment, and other information about each planting, increased the value of these observations materially.

Bernard Harkness, of the Rochester (N.Y.) Park Department, kindly made available many measurements which he has made of trees in the Rochester public parks.

We are grateful to C. A. Bickford, R. T. Bingham, R. C. Brown, M. E. Fowler, P. Godwin, H. Jaynes, R. D. Lane, E. W. Littlefield, E. J. Schreiner, A. E. Squillace, and W. E. Waters for their critical reading of the manuscript, and to E. L. Little, Jr. for his help in determining the best name for border white pine.

Possibilities of Breeding Weevil-Resistant White Pine Strains

by

Jonathan W. Wright

William J. Gabriel

JONATHAN W. WRIGHT took his B.S. degree in forestry at the University of Idaho in 1938. He received M.F., M.A., and Ph.D. degrees at Harvard University, with genetics his major field. From 1942 to 1945 he was an instructor in forestry at Purdue University. He joined the Northeastern Forest Experiment Station the following year as geneticist, headquartered at the Morris Arboretum. A recognized authority on forest genetics, Dr. Wright has published many papers both in this country and abroad. He left the Experiment Station in 1957 to become Associate Professor of Forestry at Michigan State University, East Lansing, Mich.

WILLIAM J. GABRIEL holds a B.S. degree from the University of New Hampshire, M.F. degrees from Duke and Harvard Universities, and is now completing his Ph.D. thesis as a final requirement for that degree at Harvard. A veteran of 4 years in the Air Force, he worked as forest geneticist for a year at the Maria Moors Cabot Foundation. In 1954 he joined the Northeastern Forest Experiment Station and was for 2 years at the Morris Arboretum. He was transferred in 1956 to his present post as geneticist at the Burlington, Vermont, Laboratory of the Experiment Station's White Pine-Hardwood Research Center.

Contents

THE WEEVIL PROBLEM	1
INTRODUCED SPECIES	
as sources of weevil resistance	2
Summary by species	
Armand pine	4
Border white pine	4
Himalayan white pine	5
Japanese white pine	7
Korean white pine	8
Limber pine	9
Macedonian white pine	10
Mexican white pine	12
Swiss stone pine	15
Western white pine	16
The provenance problem	19
Possibilities of using species hybrids	19
EVIDENCE OF DIFFERENCES	
in weevil resistance among geographic ecotypes of eastern white pine	20
DIFFERENCES IN RESISTANCE	
among small local populations of eastern white pine	21
SELECTION OF INDIVIDUAL	
white pine trees for resistance to the white-pine weevil	22
Independence of weeviling in successive years	24
Use of 2 x 2 contingency tables	25
Use of the Poisson distribution	26
Effectiveness of statistical and other approaches to individual tree selection	28
THE WORK INVOLVED	
in selecting and testing apparently resistant phenotypes	29
SUMMARY	31
A FINAL WORD	32
LITERATURE CITED	33

The Weevil Problem

EASTERN white pine (Pinus strobus L.) is a highly versatile species. It is easily planted, adaptable to a wide variety of soils and climates, and reproduces itself well. Also it grows rapidly and is capable of producing high-quality lumber. These characteristics once entitled white pine to a top position in the forest economy throughout much of the Northeast. Unfortunately, its susceptibility to attack by the white-pine weevil (Pissodes strobi (Peck)) now has relegated the species to the role of a second-rate or even a weed tree in some parts of the region.

The total loss of potential timber volume due to the white-pine weevil in New Hampshire alone has been estimated at 2,160,000 board-feet of sawlogs, and 151,000,000 cubic feet of other materials (27)¹. In New England and the Middle Atlantic States the average annual loss from weevil-ing is estimated at 120,000,000 board-feet of sawlogs and 31,000,000 cubic feet of other materials.² These losses can be lessened materially by spraying (5, 6, 23), pruning, or maintaining light overhead shade (15). But such measures are expensive and are applicable only in special circumstances.

If an agronomist is faced with a serious pest problem, he turns to the plant breeder for the production of a resistant strain. Plant breeders have been successful in developing disease- and insect-resistant strains in a wide variety of crop plants (21, 26). Similarly, the forester looks to the tree breeder for assistance in solving forest pest problems.

White pines are already the subject of an intensive series of studies aimed at the production of a strain resistant to the white-pine blister rust (Cronartium ribicola Fischer). The results have been most encouraging; they indicate that the goal can be achieved in a reasonable length of time by selection and breeding within species (2, 24), by the use of exotics (4, 10), or by interspecific hybridization (3, 17).

There are several published reports of inherent differences in insect resistance in forest trees. Austin et al. (1) reported that shoot characters were useful in the selection of ponderosa pines (P. ponderosa Laws.) resistant to the resin midge. Fielding (7) reported clonal differences in aphid resistance in Monterey pine (P. radiata D. Don); most of the susceptible clones were derived from susceptible parents. In California, Miller (18, 19) found that certain

¹Numbers in parentheses refer to Literature Cited.

²Northeastern Forest Experiment Station. Unpublished data.

pine hybrids were resistant to attack by the pine reproduction weevil (Cylindrocopturus eatoni Buchanan). Schreiner (25) found clonal differences in the susceptibility of Populus hybrids to attack by the Japanese beetle (Popillia japonica Newm.); the differences are especially noteworthy because the Japanese beetle is usually an omnivorous feeder. Flordh (8) reported that F_1 hybrids of Populus tremuloides Michx. X P. tremula L. were superior to either the F_2 's or the European parent in several respects--including resistance to leaf-eating insects. In Douglas-fir (Pseudotsuga menziesii (mirb.) Franco), Heitmuller (9) found clonal but not racial differences in susceptibility to Adelges cooleyi (Gill.).

The literature gives only indirect evidence on the possibilities of finding genetic resistance to the weevil in the 5-needled pines. MacAloney (15) reported that eastern white pine is severely attacked; that western white pine (P. monticola Dougl. ex. D. Don), limber pine (P. flexilis James), and foxtail pine (P. balfouriana Murray) are commonly attacked; and that Himalayan white pine (P. griffithii McClelland) is rarely attacked. Kriebel (14) reported differences in susceptibility associated with differences in bark thickness of eastern white pine.

In the summer of 1952, the senior author embarked on a series of studies to explore the possibilities of developing weevil-resistant strains of white pine and to formulate plans for the production of such strains. The junior author joined in the search for resistant material in the summer of 1955. This paper summarizes our results to date and lists the more promising possibilities for future action.

We considered that there are four possible sources of weevil resistance in the white pines--resistant species, resistant geographic ecotypes, resistant local races, and resistant individuals--and made our observations to show which of these sources indicate the most promise.

Introduced Species as Sources of Weevil Resistance

ALL species of 5-needled white pines belonging to the section CEMBRA were observed, with the following exceptions: The western American whitebark pine (P. albicaulis Engelm.) and sugar pine (P. lambertiana Dougl.), the Formosan white pine (P. formosana Hayata), and the dwarf stone pine of eastern Asia (P. pumila (Pallas) Regel). The soft

pinus of the section PARACEMBRA were not studied because of their generally poor timber form and because of anticipated difficulties in crossing the sections PARACEMBRA and CEMBRA. The 10 introduced species considered to be potential sources of weevil resistance were studied, where available, in the following arboreta and forest plantings:

- BE. Former H. W. Sargent Estate, Beacon, N. Y.
- BR. Brett Arboretum, Fairfield, Conn.
- C-8. Cattaraugus State Forest No. 8, N. Y. Elevation 1,600 feet. Planted in 1937 on a west-facing old field.
- CL. Former Cluett Estate, Williamstown, Mass.
- DEP. Durand Eastman Park, Rochester, N. Y. Elevation 600 feet.
- ES. Olmsteadville plantings, Lots 64 and 65, Hoffman Township, towns of Schroon and Minerva, Essex County, N. Y. (State Forest Preserve). Elevation 1,300 feet. Planted in 1931 on an Adirondack stony loam soil.
- GB. Swann State Forest, Great Barrington, Mass.
- HC. Haverford College Arboretum, Haverford, Pa. Elevation 300 feet.
- HP. Highland Park, Rochester, N.Y. Elevation 600 feet.
- M-1-F. Montgomery State Forest No. 1, Proposal F, N. Y. Elevation 1,300 feet; planted in 1932, 1934, and 1936.
- M-1-K. Montgomery State Forest No. 1, Proposal K, N. Y. Elevation 1,300 feet; planted in 1934.
- MO. Morris Arboretum of the University of Pennsylvania, Philadelphia, Pa. Elevation 200 feet.
- OT-10. Otsego State Forest No. 10, N.Y. Elevation 1,900 feet; planted in 1937 on a fertile old field.
- PA. Pack Forest, Warrensburg, N.Y. Elevation 800 feet; planted in 1931 on a light sandy soil. These plantings are the subject of Hirt's (1940) paper on blister rust resistance.
- S-1. Saratoga State Forest No. 1, N. Y. Elevation 900 feet; planted in 1936 on a light sandy soil.
- SW. Arthur Hoyt Scott Foundation, Swarthmore College, Swarthmore, Pa. Elevation 100 feet.
- WE. Westtown School Arboretum, Westtown, Pa. Elevation 300 feet.

The letter symbols above (BE, BR, C-8, and so on) are used below to indicate the arboreta and forest plantings in which the species was studied.

SUMMARY BY SPECIES

Some of the growth requirements and other characteristics of the species studied are described below.

Armand Pine (P. armandi Franchet)

HP, MO, SW

This species is a native of southwestern China, where it grows at elevations of 4,000 to 6,000 feet and reaches heights of 50 to 60 feet.

Young specimens at the Morris Arboretum have grown rapidly but have developed crooks as a result of winter die-back. Three 41- to 50-year-old specimens at Rochester were 45 to 50 feet tall, 12 to 19 inches in diameter, and had 5 to 7 slight crooks each when measured. The cause of these crooks is undetermined. The Armand pine starts to flower at an earlier age than the other white pines; trees have started the regular production of male strobili when 7 years old in Philadelphia and when 9 years old in Wisconsin (12). The species is reported to be resistant to blister rust (4).

Border White Pine (P. strobiformis Engelm. non Sarg., non Sudw., P. reflexa (Engelm.), P. flexilis var. reflexa Engelm.)

(M-1-F, PA)

This species occurs naturally in the mountains of southeastern Arizona, southwestern New Mexico, and northern Mexico. Its taxonomic status is confused.

The Pack Forest trees have grown slowly. At 24 years of age they were only 3 to 8 feet tall. In contrast, the Montgomery 1 plantations (of Coronado National Forest, Ariz., provenance) have grown as fast as eastern white pine. In the 22- and 24-year-old plantings, the dominant trees were 26 to 35 and 30 to 38 feet tall, 6 to 8 and 5 to 10 inches in diameter breast high, and had 0.7 and 1.3 apparent weevilings per tree, respectively. The corresponding figures for a nearby 27-year-old plantation of eastern white pine were 25 to 35 feet, 6 to 8 inches, and 1.7 weevilings per tree, respectively.

Border white pine is about as susceptible to blister rust as eastern white pine (4, 10).

The appearance of the Montgomery 1 trees indicated that this taxon is entitled to specific status. Some of the nodes were swollen. The bark on the lower trunk was very deeply ridged, like the bark of chestnut oak (Quercus prinus L.). The trees showed a high incidence of forking. Most of

these forks were narrow, as if they resulted from injury to the terminal bud before bud elongation started.

The rapid growth of this species recommends it for further attention, provided that its taxonomic status can be satisfactorily worked out and that ecotypes with better bole form can be found.

Himalayan White Pine
(P. griffithii McClel.)

(BE, HC, HP, MO, PA, SW, WE)

Himalayan white pine (fig. 1) is an important timber tree of the Himalayan Mountains. It grows from Nepal to Afghanistan at elevations of 6,000 to 12,500 feet.

The Philadelphia area has numerous 60-year-old specimens, 60 to 70 feet tall, and 1½ to 2½ feet in diameter breast high. Many of these old trees have a slight basal sweep; otherwise their bole and crown form is excellent. They have grown as rapidly, have maintained their height longer, and have self-pruned better than eastern white pine in comparable situations. These old trees produce male and female strobili in profusion.

The Philadelphia area has also many 20- to 25-year-old Himalayan white pines which are showing the excellent form and growth characters of the older trees. Some of these young trees fruit well but have not produced pollen.

The few specimens found in the Rochester parks have performed similarly. The two oldest (57 years old, 56 and 63 feet tall and 22 and 20 inches d.b.h. respectively) have grown slightly faster than nearby eastern white pine. The single Brett Arboretum specimen has grown moderately fast but is multiple-stemmed (possibly because of winter injury when young). The Pack Forest trees have grown very slowly.

Himalayan white pine seeds germinate well after stratification and the seedlings grow about as fast as eastern white pine. However, they have few fibrous roots and we have not been able to get good survival after field planting.

Our scanty data support McAloney's (15) statement that this species is rarely attacked by the white-pine weevil. Few of the Philadelphia or Rochester trees have bole crooks whereas many eastern white pine trees in those cities have crooks that were apparently caused by the weevil.

Climatic conditions within the native range of the Himalayan white pine, reports of winter killing in Philadelphia during the severe 1933-34 winter, and the poor performance of the Brett Arboretum and Pack Forest trees indicate that this species is best suited for the warmer parts of the Northeast. Possibly, however, there are hardy ecotypes that would be suited to cooler climates.



Figure 1.--*Himalayan white pine*, though commonly straight-trunked, has a slight tendency to lean.

The rapid growth, large size attained, longevity, good bole form, blister rust resistance (4), and possible weevil resistance mark the Himalayan white pine as one of the most promising of the introduced white pines for future study.

Japanese White Pine
(P. parviflora Sieb. and Zucc.)

(HC, HP, MO, SW, WE)

The Japanese white pine (fig. 2) is a native of the mountains of Japan and the Kurile Islands. In its native habitat it is a species of poor form and moderate growth rate and is of little importance for timber.

Figure 2.--The Japanese white pine is usually broad-crowned and grows moderately fast.



The largest specimen, examined in Highland Park, Rochester, was 39 years old, 48 feet tall, and 15 inches d.b.h. This tree was an excellent timber type, and appeared to be of a different ecotype than two older but smaller specimens nearby. The latter were 48 years old, 38 to 40 feet tall, 12 inches d.b.h., and had 3 to 4 apparent weevilings each. The Philadelphia area trees are growing in height at the rate of 10 to 12 inches per year. All the trees seen had medium-sized branches but very broad crowns.

Johnson (13) reported that Japanese white X eastern white pine hybrids were heavily weeviled in Wellesley, Mass. The slow growth, broad crown, and lack of proven weevil resistance do not recommend this species for intensive study.

Korean White Pine
(Pinus koraiensis Sieb. and Zucc.)
(BR, CL, GB, HC, HP, MO, PA, SW, SE)

Korean white pine is an important timber and nut tree of the mountains of Korea and Manchuria. Judging from the rigorous climate of its homeland, it should prove to be one of the hardiest white pines.

This is a rare tree in the Northeast. We saw only 16 specimens outside the Pack Forest planting. The outstanding tree examined is on the former Cluett Estate near Williamstown, Mass. It was 35 years old, 60 feet tall, 10 inches d.b.h., and had a straight bole. It had been shaded from the side by other specimen trees, and had self-pruned well. In growth rate and form, it compared favorably with eastern white pine planted on the same estate.

The Haverford, Swarthmore, Westtown, and Swann State Forest trees are younger than the Williamstown tree but are also growing rapidly and have good bole form. In contrast, the trees in the other plantings observed are growing only one- to two-thirds as fast as eastern white pine.

The seed of the Korean white pine is large (1/2 inch long) and is used as a nut in Korea. We have sampled some and found them tasty. And so have mice on four different occasions that we observed.

One apparent weeviling was seen on the Korean white pines that were examined. This indicates that the species is no more susceptible--and possibly less susceptible--to weeviling than is eastern white pine. Korean white pine is considered resistant to blister rust (4, 10).

The hardiness, large seeds, good form, and rapid growth exhibited by some specimens recommend this species for further study.



Figure 3.--In the Philadelphia area, limber pine, a Rocky Mountain species, often grows as rapidly and as straight-boled as eastern white pine. However, the lower branches of open-grown trees have an annoying tendency to turn upwards and compete with the main trunk.

Limber Pine
(*Pinus flexilis* James)

(DEP, ES, HC, HP, M-1-F, MO, PA, S-1, SN WE)

Limber pine (fig. 3) is a tree of high elevations in the Rocky Mountains. Because of its inaccessibility and branchiness, it is of minor commercial importance in its native range. It is easily distinguished from other commonly planted 5-needled pine by three characteristics: limber twigs, non-serrate needles, and a dense crown.

The limber pine seems to have wide genetic variability and no single description suffices for all the stands examined. The best trees that were measured are along a roadside near Philadelphia. These were 25 years old, 35 to 40 feet tall, straight-boled, and horizontally branched. They were superior to eastern white pine in the general vicinity in both growth rate and bole form.

Most of the Haverford trees are not so tall as comparable eastern white pine and have crooked boles, but they have surpassed eastern white pine in diameter growth.

Rochester's Durand Eastman Park trees (33 years old, 19 to 23 feet tall, 10 to 12 inches d.b.h.) have grown rapidly in diameter but not in height, and have upturned branches. In contrast, Rochester's Highland Park trees (40 to 45 years old, 42 to 50 feet tall, 11 to 17 inches d.b.h.) have grown almost as fast as eastern white pine and have horizontal branches. In the forest plantings examined most trees of this species had grown slowly.

In several plantings limber pine has shown a tendency for the lower branches to turn upward at the tips even though the leader is intact. This tendency first becomes apparent when the trees are 15 to 20 years old. As time goes on one or more of these lower branches assume the role of secondary trunks, elongating vertically at nearly the same rate as the leader, and bearing fruit as would the central trunk. The end product of this tendency is best illustrated by a 50-year-old Westtown tree, one of whose upturned branches is about a foot in diameter and is nearly as tall as the main trunk.

In the forest plantings examined there were more living blister rust cankers and more apparent blister rust mortality in limber pine than in eastern white pine. However, the incidence of infection seemed to be too small to be a limiting factor in any stand. The limber pine is considered more susceptible to blister rust than eastern white pine (4, 10).

The incidence of weeviling was very low in all the limber pine plantings studied. However, this may have been due to the small size of the forest-grown trees rather than to inherent resistance. MacAloney (15) reported that it is commonly weeviled.

Limber pine grows naturally in a region with a cool climate. Therefore, we would expect it to grow relatively better in the cooler than in the warmer parts of the Northeast. However, the opposite seems to have been true. The low-altitude Rochester and Philadelphia specimens grew faster than trees observed in the high-elevation New York State forest plantings or on the streets in Saratoga Springs, N.Y., and Pittsfield, Mass.

The rapid growth, good bole and crown form, and possible weevil resistance exhibited by some specimens recommend the limber pine for further study.

Macedonian White Pine (Pinus peuce Griseb.)

(BR, HC, HP, MO, M-1-F, M-1-K, PA, SW, SN, WE)

Macedonian white pine (fig. 4) is native in three small areas in the mountains of Greece, Bulgaria, and Yugoslavia, where it grows at elevations of 2,500 to 7,300 feet.



Figure 4.--This Macedonian white pine is typical of all those observed in the Northeast for this study--it has developed a narrow crown and fine branches.

In its native habitat it attains heights of 100 feet in 100 years, has excellent timber form, and is a valuable timber tree.

This species has survived well, has fine branches, and has developed a straight bole with little taper in all plantings that were examined. However, its growth rate has been slow to moderate, even on the best soils. The largest specimen seen, in the Brett Arboretum, was 45 years old, 40 feet tall, and 9 inches d.b.h. The fastest growing specimen seen, at Westtown, was 15 years old, 22 feet tall, and 5 inches d.b.h. These growth rates compare favorably with those of planted and native trees in Europe as reported by Muller (20).

There was a high incidence³ of needle cast caused by Hypoderma desmazierii Duby in the Montgomery 1 forest plantings. At the time of the September 1954 examinations the apical two-thirds of nearly every needle on the infected trees was brown. The fact that the branches of diseased and healthy trees were closely intermingled indicates that there are probably genetic differences in susceptibility to attack within this species. Macedonian white pines observed in other locations were free of the disease.

In the Montgomery 1-F planting, the 20-year-old Macedonian white pines had an average of 0.22 weevilings per tree as compared with an average of 2.0 weevilings per tree on nearby natural reproduction of eastern white pine. In Highland Park, Rochester, there were two apparent weevilings on seven 40- to 47-year-old trees as compared with 54 apparent weevilings on 22 nearby 55-year-old eastern white pines. These and scattered observations in other areas of light infestation indicate that the species is more resistant to the white-pine weevil than eastern white pine. The species is considered moderately susceptible to blister rust (4, 10).

The excellent timber form, rust resistance, and possible weevil resistance recommend Macedonian white pine for further study. However, because of its slow growth, it will probably find its greatest use as a parent of interspecific hybrids.

Mexican White Pine
(P. ayacahuite Ehrenb.)

(DEP, HP, WE)

Mexican white pine (fig. 5) is a taxonomically variable species of which three geographic varieties are recognized (16). Within its native range, which extends from Guatemala to northern Mexico, it is a high mountain species of considerable local importance as a timber producer.

³Identification by J. R. Hansbrough, Chief, Division of Forest Disease Research, U.S. Forest Service.

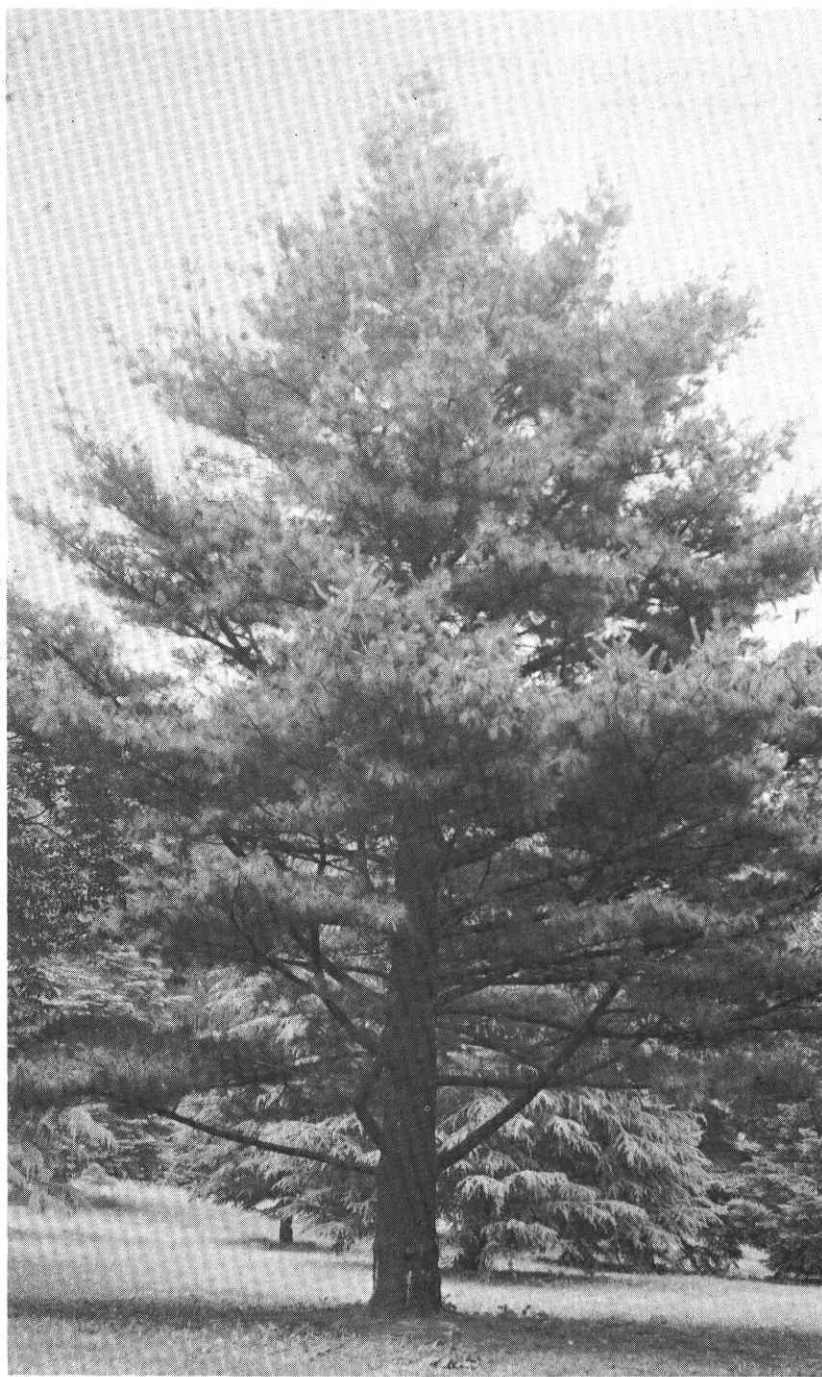


Figure 5.--*Mexican white pine*. This species has been unexpectedly hardy in the Northeast.



The true identity of the six trees we observed is in doubt. They fit the description of P. ayacahuite, yet they have been unexpectedly hardy for a Mexican species. Progeny of the Philadelphia specimen have survived Pennsylvania and Massachusetts winters unharmed, whereas seedlings that were grown from two different seedlots collected by A. G. Johnson at high elevations in the northern part of the natural range of P. ayacahuite failed to survive their first Maryland winter.

The Rochester and Philadelphia trees are similar. They have grown faster in diameter but slower in height than eastern white pine; they are straight-boled; and they produce large quantities of viable seed at frequent intervals. There are no data on weevil or rust resistance.

Though this species merits attention because of its rapid growth, considerable provenance and taxonomic research is needed before its full potentialities in the Northeast can be realized.

Swiss Stone Pine
(P. cembra L.)

(BE, HC, HP, MO, PA, SW, WE)

The Swiss stone pine (fig. 6) is distributed widely in Siberia and in the mountains of central Europe. It is likely that most of the northeastern trees belong to the typical Swiss variety (P. cembra var. cembra).

All the Swiss stone pines seen can be characterized as straight-boled, fine-branched, dense-foliaged, slow-growing, and without weevilings. The largest measured tree, on the grounds of the former H. W. Sargent estate near Beacon, N. Y., was 39 feet tall, 18 inches d.b.h., and an estimated 80 years old. The fastest growing trees measured were in Rochester, N. Y.; they were 42 years old and 32 feet tall.

Figure 6.--This Swiss stone pine with its dense, narrow crown shows good form. Unfortunately, slow growth makes it a poor timber prospect for the Northeast.

In the Northeast, the oldest and largest tree of which we have a record is on the Remington Estate, Cazenovia, N. Y. Planted in 1856, it was 59 feet tall and 26 inches d.b.h. when measured in the spring of 1957.⁴

⁴These measurements were provided by E. W. Littlefield, Assistant Director, Division of Lands, Albany, N.Y.

Despite its good timber form and resistance to blister rust (10), Swiss stone pine seems to offer little prospect as a timber tree because of its slow growth.

Western White Pine
(P. monticola Dougl. ex D. Don)

(C-8, DEP, ES, HC, HP, M-1-F, OT-10, S-1, SN, WE)

Western white pine (fig. 7) is one of the most important timber trees of the West. It grows naturally in the Sierra Nevada and Cascade Mountains of California, Oregon, and Washington, and in the northern Rocky Mountains of Idaho, Montana, and British Columbia.

This western tree offers the best immediate source of weevil resistance of any white pine species studied (see tables 1 and 2). In all the forest plantings studied, it was weeviled much less than comparable eastern white pine. Not only that, but the western trees showed excellent recovery from weeviling. Very rarely was the offset due to weeviling more than 2 inches.

Western white pine appears to be a slow starter for its first 5 or 6 years after outplanting, but after that it grows at about the same rate as eastern white pine. In the severely infested Cattaraugus 8 and Otsego 10 plantings, the western species had caught up with nearby heavily weeviled

Table 1.--Growth data for individual open grown trees of
western white pine in Pennsylvania and New York

Location of trees	Trees ¹	Age	Height	D.b.h.
	Number	Years	Feet	Inches
Haverford, Pa.	5	17	17	5.5
Westtown, Pa.	2	23	32	10.3
Saratoga, N.Y.	4	13	12	2.0
Rochester, N.Y., Durand Eastman Park	2	28	45	11.3
Rochester, N.Y., Highland Park	2	45	58	10.9

¹This column indicates the total number of trees observed at each location. The height and diameter data apply to the largest tree at each location.

eastern white pine in height but not in diameter growth at the time of these examinations. The western species was superior to the native species in height growth, diameter growth, and survival percent in the Saratoga 1 plantings.

Western white pine was superior to eastern white pine in fineness of branch and in narrowness of crown in every planting except that at Haverford College. The Haverford trees are relatively broad-crowned, large-branched, and slow-growing.



Figure 7.--The western white pine is one of the most promising exotic species. It has rapid growth, resistance to weevil attack, and excellent bole form.

This species is considered very susceptible to blister rust (4). Our observations support their conclusions. In the Otsego 10 plantation, cankers that originated before the last Ribes eradication in 1945 will probably kill 50 percent of the trees. Equally heavy mortality is expected in the Cattaraugus 8 plantation. Only in the Saratoga 1 plantations were few cankers found.

The Otsego 10 planting was made partly on a slope and partly on a wet flat. Growth and survival were good on the slope, but no western white pines survived on the flat. In contrast, eastern white pine survived on both slope and flat.

The weevil resistance, good recovery from weeviling, rapid growth, good bole and crown form, climatic adaptability, increasingly effective protection against blister rust through Ribes eradication, and progress in the breeding of rust-resistant strains mark western white pine as a very promising species for further study. Provenance tests should be established in the near future to extend our knowledge of the geographic ecotypes and soil adaptability of this species.

Table 2.--Growth and weeviling data for forest plantings of western white pine in New York State

Plantation location	Provenance	Area planted	Spacing	Age	Dominant trees		Average weeviling per tree, all trees	
					Height	D.b.h.	<u>P. monticola</u>	<u>P. strobus</u> ¹
		Acres	Feet	Years	Feet	Inches	Number	Number
Otsego 10	Kaniksu, N.F., Idaho	2.5	5x5	17	18-22	4-6	0.71	3.41
Cattaraugus 8	" "	3.0	8x8	19	22-26	4-8	.42	4.00
Saratoga 1	" "	.01	4x4	20	22-28	4-6	.04	.43
Saratoga 1	" "	2.0	6x6	20	22-28	5-8	.08	.43
Olmsteadville, Essex Co.	Wind River, Wash. (?)	.9	6x8	24	22-29	4-7	.05	.61
Montgomery 1	Washington	.2	6x6	23	25-38	6-10	.20	1.73

¹The figures for P. strobus were taken from eastern white pine stands adjacent to and of the same age as the western white pine stands studied. The dominant eastern white pines were 95 to 110 percent as tall as the dominant western white pines.

The weevil resistance and climate adaptability of western white pine seem to be well enough verified to warrant recommending its immediate use as a minor component of new plantings of eastern white pine in heavily weeviled areas. At best, assuming no blister rust damage, the western white pine can be expected to develop into high-value, well-formed crop trees. At worst, assuming heavy blister rust damage, such mixed stands will suffer light thinnings as the western species dies. For the present, Kaniksu provenance seed is recommended for such plantings.

THE PROVENANCE PROBLEM

Except for nearly all the State forest plantings, trees we observed are of unknown geographic origin. There are many questions that cannot be answered even by the most detailed study of such stock. For example, was the relatively poorer performance of the cool-climate limber pine in cool areas than in warm areas due to differences in seed origin among plantings? Is there any possibility of obtaining a better formed, hardy Mexican white pine, and if so, where? Do the present observations indicate the maximum hardiness of the Himalayan white pine?

Actually, stock of unknown origin is capable of yielding only such preliminary observations as are reported here. For future work it is imperative that all seedlings be grown from seed of certified geographic origin. The extra labor involved in assembling such seed would be very slight because there are now a large number of tree breeders, seed collectors, and seed dealers who appreciate the value of reliable source data and can make or arrange for the desired collections in almost any country.

POSSIBILITIES OF USING SPECIES HYBRIDS

The species crossability pattern of the 5-needed white pines is given in table 3. Some of the hybrid combinations listed there have outgrown their parents in nursery

Table 3.--Summary of white pine species crosses by all workers

Series and species	Series and species											
	CEMBRAE				FLEXILES			STROBI				
	koraensis	pumila	cembra	albicaulis	flexilis	strobiformis	armandi	lambertiana	ayacahuite	parviflora	peuce	griffithii
CEMBRAE												
koraensis	--	--	--	--								
pumila	A	--	--	--								
cembra	F	--	F	--								
albicaulis	F	--	F	--								
FLEXILES												
flexilis	F	--	F	--								
strobiformis	--	--	--	--	F	--	--					
armandi	U	--	--	--	U	F	--					
STROBI												
lambertiana	H	--	--	F	F	F	H					
ayacahuite	F	--	F	--	F	--	--	H	--			
parviflora	--	--	--	--	--	--	--	F	--	--		
peuce	F	--	--	--	--	--	--	F	H	H	--	
griffithii	--	--	F	--	H	--	F	F	H	H	H	--
monticola	U	--	--	--	A	--	U	F	H	H	H	H
strobis	F	--	F	F	H	--	F	F	H	H	H	H
strobis var. chiapensis	--	--	--	--	--	--	--	--	--	--	U	--
formosan	--	--	--	--	--	--	--	--	--	--	--	--

Legend: H = hybrids, U = undetermined, F = failure, A = attempted, results not yet known.

tests. Among such combinations are P. strobus X ayacahuite and reciprocal, P. strobus X griffithii and reciprocal, P. monticola X strobus, and P. flexilis X griffithii.

Other factors being equal, it seems best to concentrate future efforts on species that we know or suspect will cross with eastern white pine. By doing so we can utilize the many good characteristics of our native species and the hybrid vigor often found in species crosses. When judged on the basis of crossability relationships, probable weevil resistance, and other characteristics, western white pine, Himalayan white pine, Macedonia white pine, and Mexican white pine are, in the order named, the most promising of the introduced 5-needled pines.

Evidence of Differences in Weevil Resistance among Geographic Ecotypes of Eastern White Pine

EVIDENCE for the presence of differences in resistance to weeviling among geographic ecotypes of eastern white pine was obtained from a small provenance test in Block 13-1, Proposal FFF, Oswego 2 State Forest, in the Tug Hill area of New York. In this planting, each of four different provenances was represented by a single 2- to 4-acre plot established in 1941 on moist, moderately well-drained soils. Within ½ mile of the test are three plantations established at the same time with stock of a single (New York seedlot 14) Adirondack provenance. When examined in the summer of 1955 all plantings were of approximately equal height. The individual trees in the plantings ranged from 8 to 15 feet tall.

The trees of Eagle Lake, Ontario, provenance were weeviled much less than the trees of New York provenance, as shown in the following tabulation.

<u>Provenance</u>	<u>Trees examined (number)</u>	<u>Weevilings per tree (number)</u>
Eagle Lake, Ont.	439	0.47
St. Lawrence 10, N.Y.	365	.74
Bolton Landing, N.Y.	107	.99
North Hudson, N.Y.	131	.76
Adirondack Mountains, N.Y.	95	.81
Adirondack Mountains, N.Y.	93	.91
Adirondack Mountains, N.Y.	106	1.00

⁵Wright, J. W. Species hybridization in the white pines (manuscript in preparation).

To minimize the possibility that the observed differences in weeviling could be interpreted as due to differences in soil, aspect, or location, the numbers of weevilings were tallied on five pairs of 60 x 75 foot sub-plots in the Eagle Lake, Ont., and St. Lawrence 10, N. Y., plots; members of each pair of sub-plots were adjacent. The Eagle Lake sub-plots had 0.49, .64, .34, .42, and .30 weevilings per tree; the corresponding St. Lawrence 10 sub-plots had 0.67, 1.02, .61, .80, and .55 weevilings per tree, respectively.

Pauley, Spurr, and Whitmore (22) found that eastern white pine of three Ontario provenances suffered less weevil damage than did trees of Massachusetts, New Hampshire, or New York provenance. They attributed the differences in weeviling to differences in growth rate.

These preliminary data indicate that there may be inherent differences in susceptibility to damage by the white-pine weevil associated with differences in geographic origin. This possibility will be studied in the series of range-wide provenance tests now being undertaken by five different regional experiment stations of the U. S. Forest Service and by the Ontario Department of Lands and Forests.

Differences in Resistance among small local populations of Eastern White Pine

A THIRD part of our study included a search for local populations of eastern white pine that exhibited probable inherent differences in resistance to the white-pine weevil. The ideal situation for demonstrating the presence of such differences would be a pair of similar-aged, pure stands that are located adjacent to each other on the same soil type and that differ markedly in amount of weeviling. The stands should have similar spacings and should be young enough that all weevilings are plainly visible. Also, they should be of different but related provenance; they may be natural or planted.

These ideal conditions were not found. In Massachusetts, near Townsend, and along state highway 32 from Monson to Petersham, enough white pine was seen to permit the study of a series of adjacent stands; the adjacent stands were found to have similar amounts of weeviling. Nearly all New York plantations are of the same provenance (New York seed-lots 14 and 162, collected in Essex and Clinton Counties, N.Y.) In other northeastern states the provenance of planted stock is largely unknown.

The most striking stand differences found in amount of weeviling involved stands on wet flats and stands on well-drained slopes. In Delaware, Oswego, and Otsego Counties, N. Y., and in Litchfield County, Conn., we found six "wet flat" stands in which there had been much less weeviling and in which recovery from weevilings had been better than in the nearest comparable upland stand. These differences are best interpreted as due to environment rather than to heredity unless we make the unlikely assumption that there is a single, widespread, "wet flat" ecotype.

In the lightly weeviled (0.2 to 0.9 weevilings per tree in 15- to 30-year-old stands) valley along N.Y. highway 43 near Gallupville, Schoharie County, N. Y., and in the heavily weeviled (about 3.5 weevilings per tree in 20-year-old stands) area around Oneonta, Otsego County, N. Y., there were opportunities for comparison of natural stands with plantations of Essex and Clinton Counties provenance. In both cases natural stands and nearby plantations had similar amounts of weeviling.

The most critical evidence on the presence or absence of local races which differ in weevil resistance came from three young plantations in the Tug Hill area of New York. These are of the same Essex and Clinton County provenance stock planted elsewhere in the state and are situated within a radius of 1.1 miles. Yet current weeviling in the three plantations was 3, 12, and 79 percent in 1954. These differences between genetically similar stock are as extreme as any found in the region. In other words, the observed variation could have all been environmental.

These results are disappointing. They indicate that possible inherent stand differences in resistance to weeviling will be extremely difficult to recognize in the field, and that further intensive field search would be unrewarding. Such differences could probably be detected only by an intensive and well-replicated series of progeny tests.

Selection of Individual White Pine Trees for Resistance to the White-Pine Weevil

CHOOSING PROPER SAMPLES

AT BEST the development of a weevil-resistant strain of eastern white pine by selection and crossing of individual trees promises to be a long and difficult task. Extreme care in making the selections is essential; one man-year spent in selection may not only increase the chances of ultimate success but also may save 2 or 3 man-years of testing time.

In studying individual tree variation within stands we tried to make our samples as homogeneous as possible and paid particular attention to the following factors.

Absolute height.--Stands that are 10 to 30 feet tall are the best for study. There has been too little opportunity for weeviling in stands less than 10 feet tall, and weevilings are difficult to see in trees that are more than 30 feet tall. Also, it is difficult to visualize all the weevil-influencing factors in the past history of an old stand.

Relative size.--Within a stand, the taller and more vigorous trees are more susceptible to weeviling than the smaller trees. Therefore, a sample should include only the trees within a certain height or dominance class in even-aged stands. In young, open, natural stands we found it desirable to study the largest size class in which there was an adequate number of trees on a uniform area, ignoring the relatively few large trees and the small trees dominated by nearby larger trees.

Stand purity.--It is best to sample pure pine stands because the presence of overhead or side shade lessens the probability that a tree will be weeviled.

Spacing.--All trees included in a sample should have had sufficient growing space to develop a vigorous crown with its top exposed to full sunlight on all sides.

Soil and topography.--No obvious differences in soil or topography should be included within a single sample. For example, even the smallest stand should be considered as two separate samples if it includes a flat and a slope.

Intensity of weeviling.--The objective of this preliminary work was twofold--(1) to identify probable hereditary variation in resistance to weeviling and (2) to select trees for future breeding work. Stands with a low intensity of weeviling can often be used to satisfy the first objective, but stands with heavier weeviling must be used for the second.

The intensity of weeviling can probably be increased by artificial caging experiments. This practice may or may not be useful in preliminary selection work, depending on cost (selection work involves thousands of trees) and uniformity of results.

Provenance.--Data from natural or planted stands of a known provenance is much more useful than data from stands of an unknown source. Selection work in a plantation of unknown provenance can yield only the few selected trees in that stand. In contrast, selection work in a natural stand can yield selected trees in that stand and additional selected trees in neighboring, related stands. Records that permit return to the vicinity of a promising find have been very profitable in western white pine. In that species,

drainage areas yielding one rust-free phenotype have on further search been found to yield 5 to 40 rust-free phenotypes; in a few drainage areas the yield was nil.⁶

Nearly all the forest plantations of eastern white pine in New York are of the same known provenance. The decision to neglect or stress all plantations in the state can thus be based on examination of a few.

Recognition of weevil damage.--In trees up to 30 feet tall, crooks caused by weevils can be distinguished easily from crooks caused by other agencies by the persistent stub with its weevil emergence holes. Unbiased errors in scoring tend to decrease the statistical precision of the results but do not lead to the assumption of more variability than is actually present. Only one main stem per tree should be scored for weevil damage in order that sampling will be from as nearly a homogeneous population as possible.

Number of trees.--Samples of at least 100 trees each --and preferably 200 trees each--are needed if data are to be evaluated statistically. Smaller samples usually give unsatisfactory results. However, there are theoretical conditions under which valid selections could be made in small samples. For example, a tree breeder would probably be justified in selecting the unweeviled tree in a 5-tree group if the other four trees had five weevilings each. We found no such groups.

Area.--Variability in the density of the weevil population, variability in soil and topography, and the small size of most suitable white pine stands combined to limit the size of the sample areas available. In actual practice we found it desirable to limit each sample to an area only 1 or 2 acres in size.

INDEPENDENCE OF WEEVILING IN SUCCESSIVE YEARS

Some evidence on migrating habits of the white-pine weevil indicates that weeviling might be dependent on whether or not a tree was weeviled the previous year. Weevils usually overwinter in the duff below the tree from which they have emerged. In addition, more weevils have been trapped in the spring from trees that were weeviled the previous year.⁷ Consequently, a test of the independence of weeviling was made, using Chi-square in a 2 x 2 contingency table. As the Chi-squares from several such tests were small enough to be random, it is concluded that weeviling in one year is not associated with weeviling the preceding year (table 4).

⁶R. T. Bingham, personal communication.

⁷Unpublished information from Forest Disease and Insect Laboratory, Northeastern Forest Experiment Station, New Haven, Conn.

Table 4.--Apparent independence of weeviling in current year
and in immediately preceding year

Location of stand: county, state	Trees observed	Percentages of trees that were weeviled in the year of exam- ination and in the immediately previous year were--		Chi- square
		Weeviled ¹	Not weeviled ¹	
	Number	Percent	Percent	
Renssalaer, N.Y.	117	27.2 (28.2)	28.4 (28.2)	0.00
Schoharie, N.Y.	240	13.6 (16.7)	17.0 (16.7)	.06
Otsego, N.Y.	149	69.6 (71.1)	72.6 (71.1)	.03
Otsego, N.Y.	120	52.6 (53.5)	53.4 (53.5)	.00
New Haven, Conn.	56	25.0 (28.6)	28.8 (28.6)	.00
New Haven, Conn.	54	50.0 (58.3)	67.8 (58.3)	1.11
New Haven, Conn.	68	33.3 (35.3)	36.4 (35.3)	.00
Franklin, Mass.	76	.0 (7.9)	8.6 (7.9)	.00
Cheshire, N.H.	72	.0 (9.7)	11.3 (9.7)	.00

¹Expected percentages are in parentheses. The expected percentages were calculated on the assumption that there was no correlation between weeviling in successive years.

For the sake of brevity, the data contained in the 2 x 2 contingency tables were reduced to the form shown in tables 4 and 5. The method by which this was accomplished can be shown by reference to the data from the Renssalaer County, N.Y., stand given in table 4. Of 117 trees examined, 33 (28.2 percent) were weeviled in 1955. This was the expected percentage of 1955 weeviling among trees that had been or had not been weeviled in 1954. The actual percentages--27.2 and 28.4 percent, respectively--were computed from the ratios $9/33$ (9 = number of trees weeviled in 1954 and 1955; 33 = number of trees weeviled in 1954) and $24/84$ (24 = number of trees weeviled in 1955 but not in 1954; 84 = number of trees not weeviled in 1954).

USE OF 2 X 2 CONTINGENCY TABLES

A tendency for the weevil to oviposit in the same tree from which it emerged would cause the weeviling of individual trees in two successive years to be positively correlated. On the other hand, genetically or environmentally induced resistance to weeviling would cause a positive correlation between weeviling in the year of examination and in all previous years.

The numbers of trees that were weeviled or not weeviled in the year of examination and in all previous years were determined by 2-foot height classes in 14 stands (table 5). The trees studied were 6 to 15 feet tall and had been exposed to weeviling for 3 to 13 years. The stands had averages of less than one weeviling per tree. This was too

Table 5.--Apparent association of weeviling in the current year
and in all previous years

Location of stand: county, state	Trees observed	Percentages of trees that were weeviled in the year of examination and that in previous years were--		Chi- square
		Weeviled	Not weeviled	
	Number	Percent	Percent	
York, Maine				
(4-6 feet tall)	132	0.0 (1.6) ¹	1.5 (1.6) ¹	0.00
(6-8 feet tall)	109	44.0 (13.0)	3.6 (13.0)	24.75*
(8-10 feet tall)	124	50.0 (25.0)	13.1 (25.0)	17.76*
(10-12 feet tall)	65	52.0 (27.7)	12.5 (27.7)	10.17*
York, Maine				
(4-6 feet tall)	148	35.7 (8.8)	5.8 (8.8)	2.42
(6-8 feet tall)	112	57.2 (13.0)	10.5 (13.0)	1.79
(8-10 feet tall)	73	33.3 (19.2)	17.2 (19.2)	.22
(10-12 feet tall)	54	47.6 (22.2)	6.1 (22.2)	10.38*
York, Maine				
(4-6 feet tall)	63	44.4 (30.2)	24.4 (30.2)	1.63
(6-8 feet tall)	75	69.8 (68.0)	58.3 (68.0)	.22
Renssalaer, N.Y.	97	28.8 (24.7)	18.4 (24.7)	.88
Albany, N.Y.	240	25.5 (16.7)	14.5 (16.7)	2.60
Otsego, N.Y.	149	69.1 (71.1)	76.1 (71.1)	.48
Otsego, N.Y.	120	64.6 (53.3)	40.0 (53.3)	6.06**
New Haven, Conn.	57	28.8 (29.6)	33.3 (29.6)	.00
Franklin, Mass.	76	40.0 (7.9)	3.0 (7.9)	2.71
Carroll, N.H.	100	24.6 (23.0)	20.5 (23.0)	.35
Hillsboro, N.H.	99	36.6 (35.9)	33.3 (35.9)	.00
Rockingham, N.H.	147	13.4 (20.8)	26.3 (20.8)	2.97
Rockingham, N.H.	82	25.0 (36.6)	40.3 (36.6)	.92
Rockingham, N.H.	73	23.6 (27.4)	34.3 (27.4)	.52

¹ Expected percentages are in parentheses. The expected percentages were calculated on the assumption that there was no correlation between weeviling in successive years.

*Significant at the 1-percent level.

**Significant at the 5-percent level.

little weeviling to justify trying to test the applicability of the Poisson distribution.

In three stands, the actual and expected distribution patterns differed significantly. The greater than expected variation in those three stands is possibly due to genetic variation among trees.

USE OF THE POISSON DISTRIBUTION

If the variation in weevilings is due to random causes, either the binomial or the Poisson distribution describes the distribution of weevilings within a small uniform stand. We used the Poisson distribution because (1) it is easier to use, and (2) it is more discriminating (that

is, it permits the recognition of biologically significant variations with a greater degree of certainty).

The distribution of weevilings was determined in seemingly uniform 100- to 400-tree samples in forty-nine 12- to 30-foot stands having averages of 1.4 to 4.0 weevilings per tree. The stands were located in Litchfield, New Haven, and Tolland Counties, Conn.; Cumberland and York Counties, Me.; Middlesex and Worcester Counties, Mass.; Cheshire, Merrimack, and Rockingham Counties, N. H.; and in Otsego and Schoharie Counties, N. Y. One of the Otsego County, N. Y., stands was a plantation of Essex-Clinton County provenance; the rest were natural. A Chi-square test was used to determine the presence of significant deviations between the observed distribution and the proper Poisson distribution for each sample.

Table 6.--Observed and expected (following the Poisson distribution)
numbers of weeviled trees in stands having significant excesses
of lightly weeviled trees

Weevilings per tree	Trees in		
	1Stand No. 1	2Stand No. 2	
		8- to 10- inch trees	10- to 12- inch trees
<u>Number</u>	<u>Number</u>	<u>Number</u>	<u>Number</u>
0	65 (60.5) ³	45 (23.5) ³	20 (12.2) ³
1	33 (52.2)	26 (37.2)	9 (16.0)
2	44 (23.0)	22 (29.4)	6 (10.7)
3	2 (6.6)	9 (15.3)	6 (4.7)
4	0 (1.4)	7 (6.1)	1 (1.9)
5	0 (.3)	5 (1.9)	4 (.4)
6	(.0)	0 (.5)	0 (.1)
7	--	(.1)	(.0)
8	--	(.0)	--
9	--	--	--
	144 (144.0)	114 (114.0)	46 (46.0)
Mean weevilings per tree	0.88	1.31	1.37
d.f.	2	3	2
	29.31*	26.65*	10.09*

¹Stand No. 1 was a 35-year-old, 35- to 40-foot tall, crowded, pure stand on a flat 8 miles east of Schoharie, Schoharie County, N. Y.

²Stand No. 2 was a 35- to 40-year-old, closed, pure stand on the Massabesic Experimental Forest, Alfred, York County, Maine.

³Expected numbers are in parentheses.

*Significant at the 1-percent level.

In 47 of the 49 stands studied, the deviations of the actual from the expected distribution patterns were not significant. In the other two stands they were significant (see table 6). Such significant deviations are interpreted as weak evidence for inherent variation in those stands. The evidence is weak because (1) significant deviations are expected in one of every 20 stands, and (2) both stands were older and more variable than is ideal for selection work.

EFFECTIVENESS OF STATISTICAL AND OTHER APPROACHES TO INDIVIDUAL TREE SELECTION

There are approaches to the selection of individual weevil-resistant trees other than the ones already discussed; all depend upon comparisons within uniform, unbiased samples. Comparisons between unweeviled intermediate and weeviled dominant trees, between trees in mixed and pure stands, or between trees in areas of widely different weeviling intensity will not lead to successful selection work. Nor will comparisons of a few trees that are the remnants of a stand logged under unknown conditions, such as the stand studied by Holst (11).

One approach is a simplification of the "Poisson" method already described. A fairly valid estimate of the average amount of weeviling in a stand can be obtained quickly from a small sample of 50 to 75 trees. After this estimate is obtained, the observed and expected (according to the binomial or Poisson distribution) frequencies of unweeviled and once-weeviled trees can be determined and compared statistically by means of a Chi-square test. This approach involves little more time than does merely looking at the trees.

Increasing the intensity of weeviling by artificial caging experiments is a refinement rather than a different approach. If caging results in a uniform increase in amount of weeviling, it will lead to more efficient phenotypic selection by decreasing the number of environmentally induced "escapes". However, if caging results in a variable increase in weeviling it may lower the efficiency of the phenotypic selection.

Another approach might be termed the "tallest--next tallest". On the assumption that the tallest trees are most subject to weeviling, a situation in which the tallest trees have been weeviled less than the next tallest trees indicates the probable presence of variations in inherent resistance in the stand. We found this situation only in the Otsego 10 State Forest planting of western white pine. This approach is hard to use in eastern white pine because of the difficulty of observing large numbers of boles and tree tops simultaneously.

The "correlated character" approach might also be termed the "causative mechanism" approach. Here the investigator tries--as Kriebel (14) did in his studies of the correlation between bark thickness and weeviling--to determine the causative mechanism underlying resistance by a study of various correlated characters, and to select directly for resistance. As Painter (21) remarked, "A knowledge of the cause of resistance is highly desirable but it may or may not be of use in breeding operations," and "Any association between an assigned cause and resistance should be complete." This approach may increase knowledge about the insect's ecology without hastening the assembling of genetically resistant material.

The traditional or "practiced-eye" approach involves diligent search by a man capable of recognizing differences and of making mental allowances for the roles played by environment and chance in causing these differences. The statistical approaches, extensions of this method, provide supporting evidence. They tell the investigators how many lightly weeviled trees to expect due to chance and prevent him from getting excited about the occasional unweeviled tree that should be expected.

The Work Involved in Selecting and Testing Apparently Resistant Phenotypes

FOR the present, western white pine seems to be the best source of weevil resistance. However, it is a relatively untested exotic and it might not prove adequately adapted to northeastern conditions. Therefore it seems desirable to at least consider an intraspecific selection and breeding program in eastern white pine and to make estimates of the amount of time involved in such a program.

Such an intraspecific breeding program would involve the following steps through the end of the second generation: phenotypic selection of 500 apparently resistant individuals; determination of the general combining ability of all 500 parents by one-parent progeny tests; determination of specific combining ability of the best 32 parents by diallel, two-parent progeny tests; phenotypic selection in the F_1 test plantations; determination of the general combining ability of the 500 best F_1 seedlings by one-parent progeny tests; and determination of the specific combining ability of the 32 best parents by diallel, two-parent progeny tests.

The number 500 was chosen for the number of parents in each generation on the assumption that the heritability of weevil resistance is either low or moderate and that therefore a large number of parents must be tested to recover 10 with adequate ability to transmit resistance to their progeny. We wish to recover at least 10 good parents in order to avoid the growth decrease that accompanies inbreeding. The number 32 was chosen as the number of best parents to include in a diallel crossing program because 32 parents crossed in all possible combinations produce $32 \times 21/2 = 496$ or approximately 500 progenies.

We spent about 32 man-days examining 64 stands, of which 5 contained possible inherent variation in weevil resistance and an estimated 15 apparently resistant phenotypes. At that rate the phenotypic selection of 500 parents would

require about $500 \times 32/15 = 1,065$ man-days or approximately $4\frac{1}{2}$ man-years. Probably less time would be required if one man were to keep on the work steadily. Even so, the phenotypic selection would take considerable time, and would be the major cost item in the program.

The collection and extraction of seeds from each of the 500 selected parents would require about 2 or 3 man-months in the parental generation. The time involved in the F_1 generation would be somewhat less because the F_1 trees would be more conveniently located in test planting.

In Philadelphia the control-pollinating season for eastern white pine is 4 or 5 days long. On each of those days one man can make from 30 to 50 different tree X tree combinations. At that rate one man could make the 496 tree X tree combinations required for each two-parent progeny test in two or three seasons. However, because of the high percentage of failures and the necessity for travelling between parents, it would be better to plan on having four men in three different pollinating seasons.

If the progenies were planted in a randomized block design with 100 replications, each replication containing 1 seedling from each parent, and were observed for 4 years after the start of weeviling, it would be possible to detect the significance of differences between progeny means of about 5 percent. Because the "minimum detectable difference" should certainly be no more than 5 percent it would be necessary to use the most efficient, 1-tree-per-plot design. Labelling of each of 50,000 trees would probably require 2 or 3 man-months; outplanting would probably require 5 to 6 man-months because, once labelled, the trees can be planted as rapidly for experimental purposes as for commercial purposes. Maintenance for 10 years would probably require 2 man-months and evaluation at the end of 10 years would probably require 1 man-month. Totalling these figures we arrive at an estimate of approximately one man-year for the establishment, maintenance, and evaluation of each test planting. For a 2-generation project four such large test plantings would be necessary.

As yet there are no data on inheritance to indicate how long such a project would have to be continued to produce a truly worthwhile new strain. Data from crop plants indicate a minimum of four or five generations but perhaps eight or ten generations would be needed.

These estimates include no time spent on vegetative propagation. Clonal tests of the parents would do no more than show the presence or absence of genetic variation in the parental population; they could not provide data on the all-important question of how well the parents transmitted resistance to their progeny. If certain parents did show exceptional transmitting ability, would it not be desirable to vegetatively propagate those parents so that the same crosses could be repeated on a large scale in seed orchards? No, because if, as hoped, the F_1 work established a correla-

tion between phenotype of the parent and the F₁ progeny means, there would be every reason to believe that the F₁-F₂ correlation would be even greater. If such a parental-F₁ correlation were not proved, the entire project would be considered a failure. At any and all stages genetic progress would be faster if we worked entirely with seedling progenies than if we included clonal tests.

Summary

IN 1952 the Northeastern Forest Experiment Station undertook a series of studies designed to explore the possibilities of developing strains of white pines that would be resistant to the white-pine weevil. These studies included examinations of 10 introduced white pine species in arboreta and forest plantings and investigations of geographic variation, local variation, and individual tree variation in eastern white pine (Pinus strobus L.).

Western white pine (P. monticola Douglas ex D. Don in Lambert) shows the most immediate promise as a source of weevil resistance. It was studied in 10 arboreta and forest plantings in New York and Pennsylvania. In all locations this species showed good climatic adaptability, growth rate, and bole form. It crosses easily with eastern white pine, is much less susceptible to the weevil than that species, but is susceptible to blister rust. For the present it can be recommended for limited use in mixed plantings in areas subject to heavy weevil attack but with light Ribes populations.

The three next most promising introduced white pines are, in the order named, Himalayan white pine (P. griffithii McClel.), Macedonian white pine (P. peuce Griseb.), and Mexican white pine (P. ayacahuite Ehrenb.). Each has desirable growth, form, or disease-resistance characteristics. However, their weevil resistance and ecotypic variation patterns must be investigated more intensively before they can be recommended for other than experimental use.

In a small unreplicated provenance test of eastern white pine, trees of Ontario provenance were found to be weeviled less than trees of New York provenance.

No data showing differences in inherent resistance to weeviling among local races of eastern white pine were obtained. On the contrary, the presence of extreme differences in weeviling incidence among three genetically similar plantations located near each other indicates that apparently resistant local races would be difficult to recognize in the field.

In eastern white pine the study of individual tree variation in inherent resistance to weevil attack was divided into three parts: (1) In nine young stands there was no correlation between weeviling of individual trees in two successive years, indicating that the incidence of weeviling follows a Poisson distribution. (2) In 3 of 14 young stands studied there was a significant positive correlation between whether a tree was weeviled in the current year and in any previous year; this was interpreted as evidence of genetic variation in weevil resistance within those 3 stands. (3) In 2 of 49 older stands studied the numbers of unweeviled trees were significantly greater than was expected due to chance alone if the incidence of weeviling follows the Poisson distribution; this was interpreted as weak evidence of genetic variation in weevil resistance within those two stands.

The possibility of developing a weevil-resistant strain by intra-ecotypic selection and breeding within eastern white pine seems remote. The testing of different geographic ecotypes within that species holds more promise, but as yet it is too early to say whether any of the ecotypes contain enough resistance to make such a project worthwhile. On the other hand, western white pine and probably other introduced 5-needled pines contain enough proven resistance to form the basis of weevil-resistant strains with desirable growth characters. The present unimproved western white pine can be recommended for some areas that have high weevil populations. The favorable results of investigations carried on elsewhere indicate that the western white pine can be used alone or in hybrid combination with eastern white pine for the production of heterotic, rust-resistant, weevil-resistant, well-formed strains adaptable to a variety of Northeastern site conditions.

A Final Word...

The production of a white pine that is genetically resistant to the white-pine weevil is a worthwhile undertaking, but it cannot be started until we have sources of resistant germplasm. The study reported in this paper was our first attempt to locate and evaluate such sources. The evaluation of western white pine as being genetically more resistant than eastern white pine in New York was an easy matter. The evaluation of inherent resistance differences within eastern white pine was not an easy matter. It required the adaptation of statistical techniques used in the genetics of other organisms to tree populations. The techniques are standard, but the manner in which they are adapted to the study of different populations is not. Therefore, we regard many of the conclusions reached as tentative and controversial. We invite comments on either the improved utilization of data from existing plantings or on the planning of efficient future research to test the validity of the tentative conclusions.

--THE AUTHORS

Literature Cited

- (1) Austin, L., Yuill, J. S., and Brecheen, K. G.
1945. Use of shoot characters in selecting ponderosa pines resistant to resin midge. *Ecology* 26: 288-296.
- (2) Bingham, R. T., Squillace, A. E., and Duffield, J. W.
1953. Breeding blister-rust resistant western white pine. *Jour. Forestry* 51: 163-168.
- (3) ----- Squillace, A. E., and Patton, R. F.
1956. Vigor, disease resistance, and field performance in juvenile progenies of the hybrid Pinus monticola Dougl. x Pinus strobus L. *Ztschr. f. Forstgenetik u. Forstpflanzenzüchtung* 5: 104-112.
- (4) Childs, T. W., and Bedwell, J. L.
1948. Susceptibility of some white pine species to Cronartium ribicola in the Pacific Northwest. *Jour. Forestry* 46: 595-599.
- (5) Connola, D. P., McIntyre, T., and Yops, C. J.
1955. White pine weevil control by aircraft spraying. *Jour. Forestry* 53: 889-891.
- (6) Crosby, David.
1950. Concentrated lead arsenate spray for control of white pine weevil. *Jour. Forestry* 48: 334-336.
- (7) Fielding, J. M.
1953. Variations in Monterey pine. *Australia Forestry and Timber Bureau Bul.* 31. 43 pp.
- (8) Flordh, S.
1954. Studier av några F₂-populationer av hybridasp. (Studies on some F₂ populations of hybrid aspen. In Swedish.) Svenska Skogsvårdsfören. *Tidskr.* 52: 287-298.
- (9) Heitmüller, von H.-H.
1954. Beobachtungen über Individuelle resistenz gegen Gilletteela cooleyi Gill. an Douglasie. (Observations on the individual resistance to G. cooleyi in Douglas-fir. In German: English summary.) *Ztschr. f. Forstgenetik u. Forstpflanzenzüchtung* 3: 99-100.
- (10) Hirt, Ray, R.
1940. Relative susceptibility to Cronartium ribicola of 5-needled pines planted in the East. *Jour. Forestry* 38: 932-937.

- (11) Holst, M.
1955. An observation of weevil damage in Norway spruce. Canad. Dept. Northern Affairs and Nat. Resources, Forestry Br., Forest Res. Div. Tech. Note 4: 3 pp.
- (12) Johnson, A. G.
1947. Sexual maturity in two white pine species. Jour. Forestry 45: 827.
- (13) -----
1952. Spontaneous white pine hybrids. Jour. Arnold Arboretum 33: 179-185.
- (14) Kriebel, H. B.
1954. Bark thickness as a factor in resistance to white pine weevil injury. Jour. Forestry 52: 842-845.
- (15) MacAloney, H. J.
1943. The white-pine weevil. U.S. Dept. Agr. Cir. 221. 31 pp.
- (16) Martinez, Maximino.
1948. Los pinos Mexicanos. Ed. 2. 361 pp. Ediciones Botas, Mexico City, Mexico.
- (17) Meyer, H.
1954. Der Bastard Pinus strobus x excelsa. (The hybrid P. strobus x excelsa. In German.) Internatl. Cong. Union Forest Res. Organ. Proc. 1953, Sect. 22, No. 13. 2 pp. Rome.
- (18) Miller, J. M.
1947. Hybrid pine may prove answer to pine weevil menace. The Timberman 48 (11): 52, 54, 56.
- (19) -----
1950. Resistance of pine hybrids to the pine reproduction weevil. U.S. Forest Serv. Calif. Forest and Range Expt. Sta., Forest Res. Note 68. 17 pp.
- (20) Muller, Karl M.
1932. Pinus peuce, the Macedonian white pine, as a substitute for Pinus strobus. Blister Rust News 16: 62-69.
- (21) Painter, R. H.
1951. Insect resistance in crop plants. 520 pp. MacMillan, New York.
- (22) Pauley, Scott S., Spurr, S. H., and Whitmore, F. H.
1955. Seed source trials of eastern white pine. Forest Sci. 1: 244-256.
- (23) Rhodes, Arnold D.
1956. Comparison of lead arsenate, methoxychlor, and benzene hexachloride for control of white-pine weevil. Jour. Forestry 54: 134-135.

- (24) Riker, A. J., and Patton, R. F.
1954. Breeding of Pinus strobus for quality and resistance to blister rust. Univ. Wis. Forestry Res. Note 12. 2 pp.
- (25) Schreiner, E. J.
1949. Poplars can be bred to order.
In Trees, U.S. Dept. Agr. Yrbk, 1949: 153-157.
- (26) Snelling, Ralph O.
1941. Resistance of plants to insect attack.
Bot. Rev. 7: 543-586.
- (27) Waters, W. E., McIntyre, T., and Crosby, D.
1955. Loss in volume of white pine in New Hampshire caused by the white-pine weevil. Jour. Forestry 53: 271-274.