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 (*Piruculаria 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.

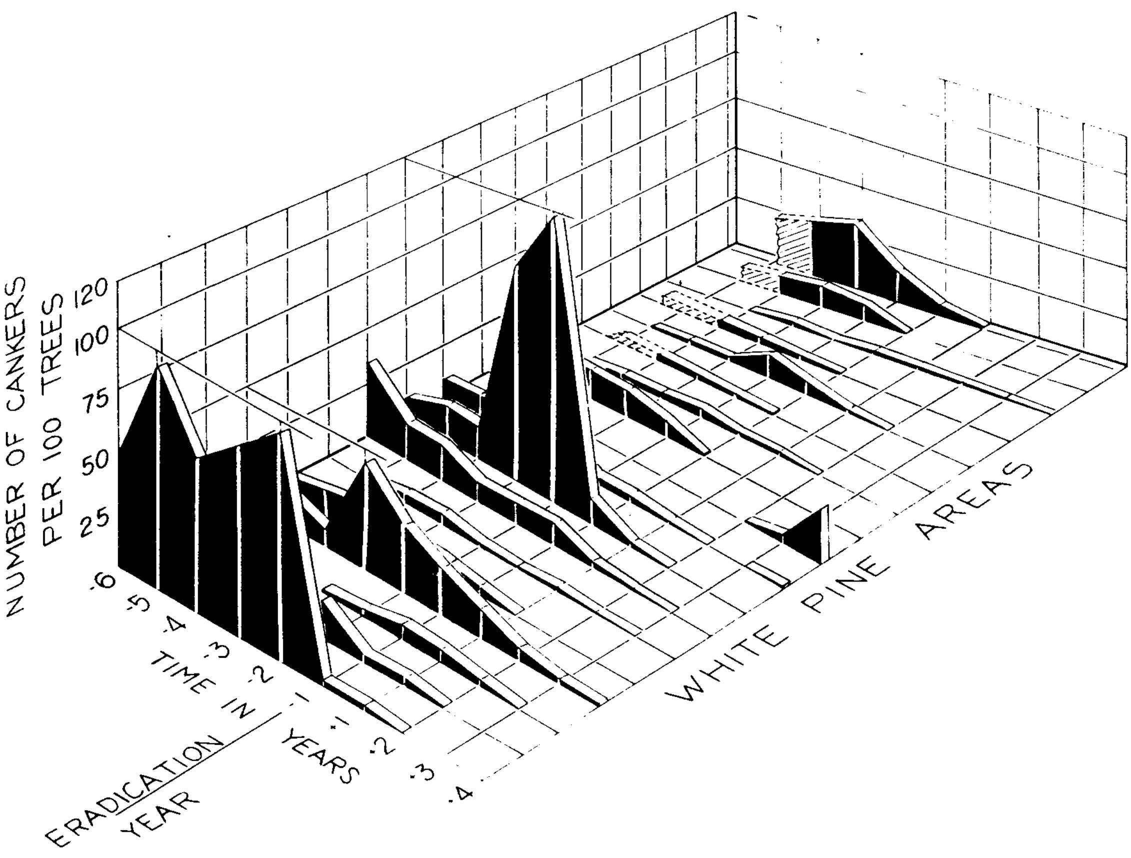

Figure 1. Differences in the amount of blister rust infection occurring on 18 of 29 study areas.

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.

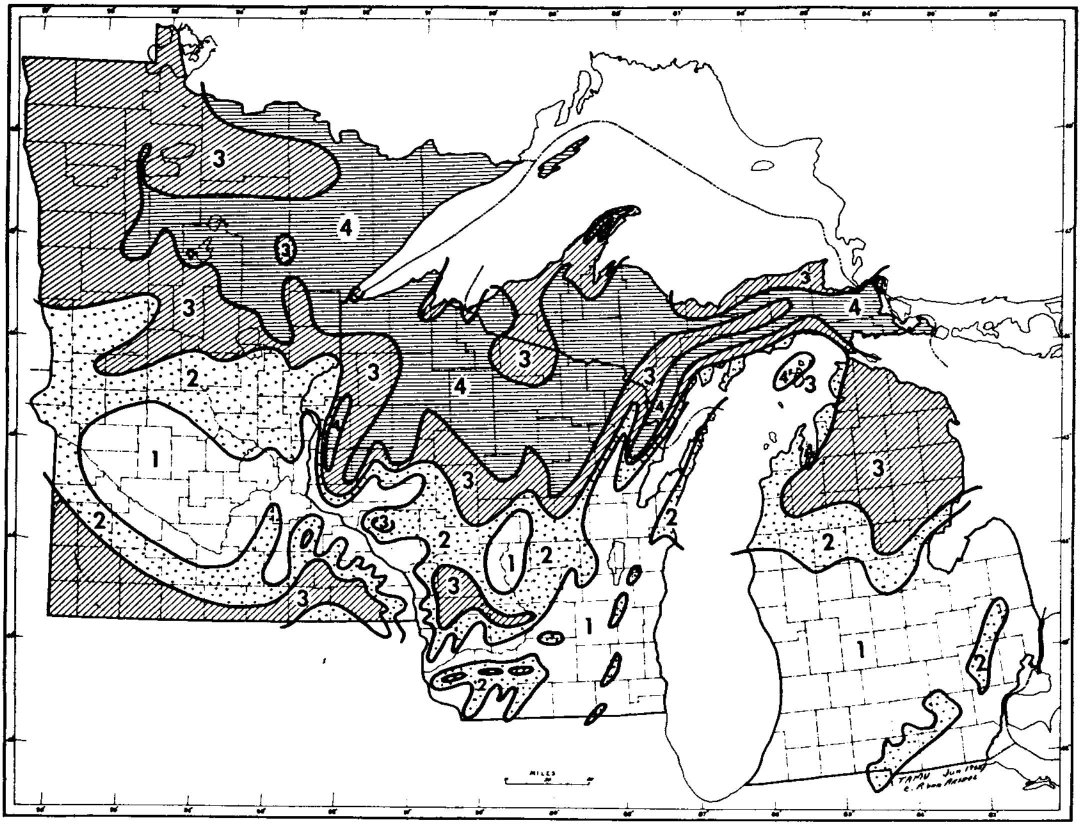

Figure 2. Map showing differences in quantity of blister rust spread to white pines in the Lake States. Rust in tops of emergent pines carried from distant ribes are characteristic of Zone 4. The cooler the summer weather, the more favorable for disease spread.

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.

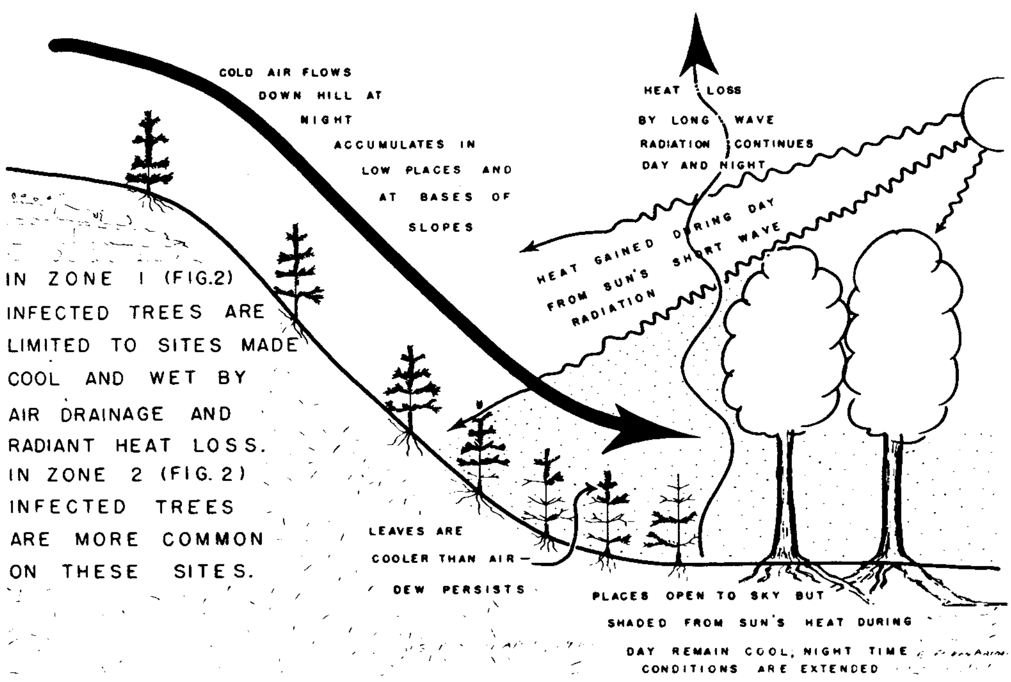

Figure 3. Drainage of cold air at night and radiant heat loss make locally cool wet spots.

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.

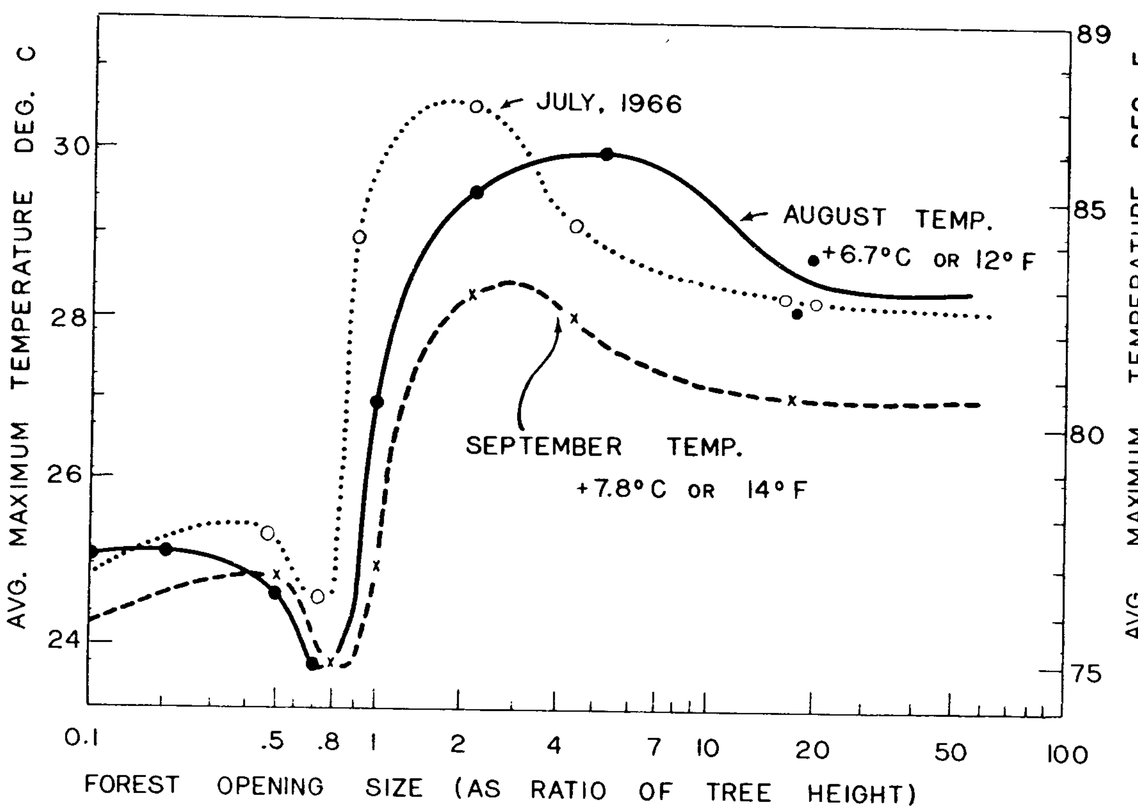

Figure 4. The relative effects of circular forest opening diameter and air temperature in the center of the opening (18" above the ground).

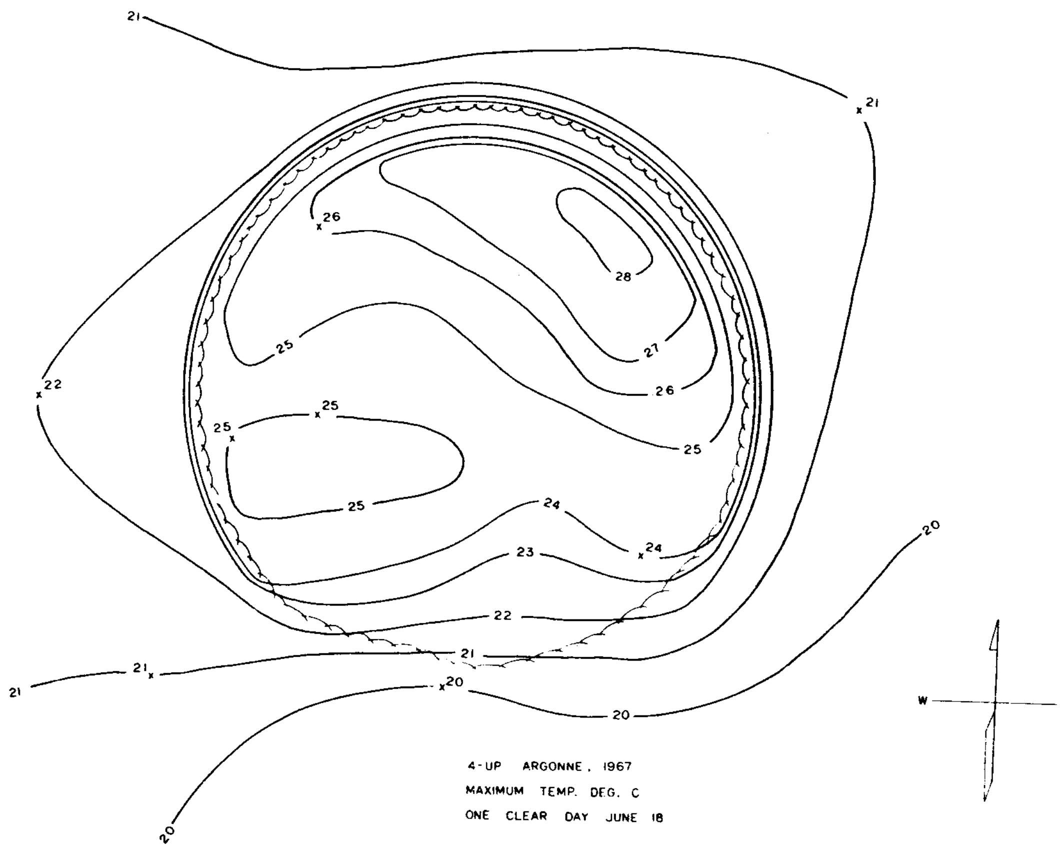

Figure 5. Temperature variations in a forest opening 280 ft. in diameter in 70 ft. tall trees (4:1::D:H ratio). The 8°C warming above the shade temperature would raise a July or August day temperature of 27°C to 35°C--a temperature fatal to blister rust.

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.

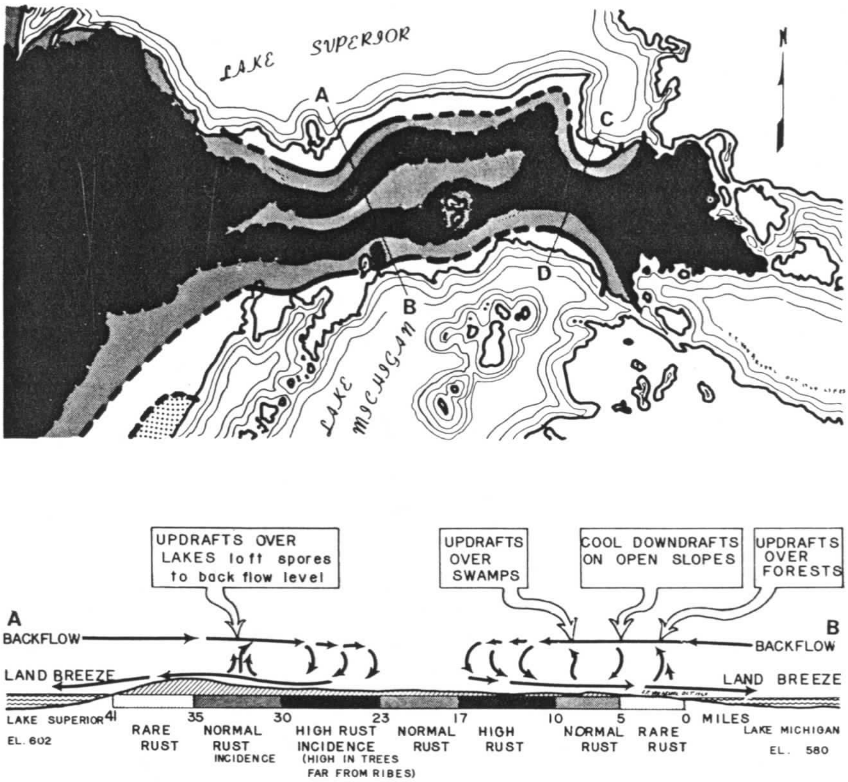

Figure 6. Map of eastern Upper Michigan showing areas of high blister rust (high in trees, far from ribes). Darkest area has high rust. Lower diagram shows cross section of airflows controlling rust spread in this area.

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

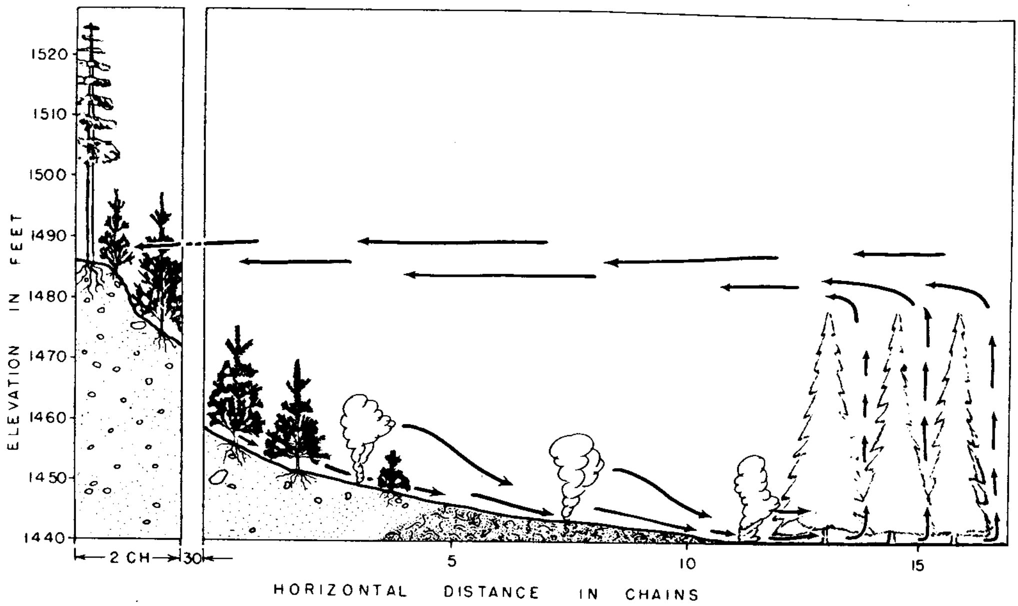

Figure 7. Pattern of airflow that controls rust spread around a swamp edge.

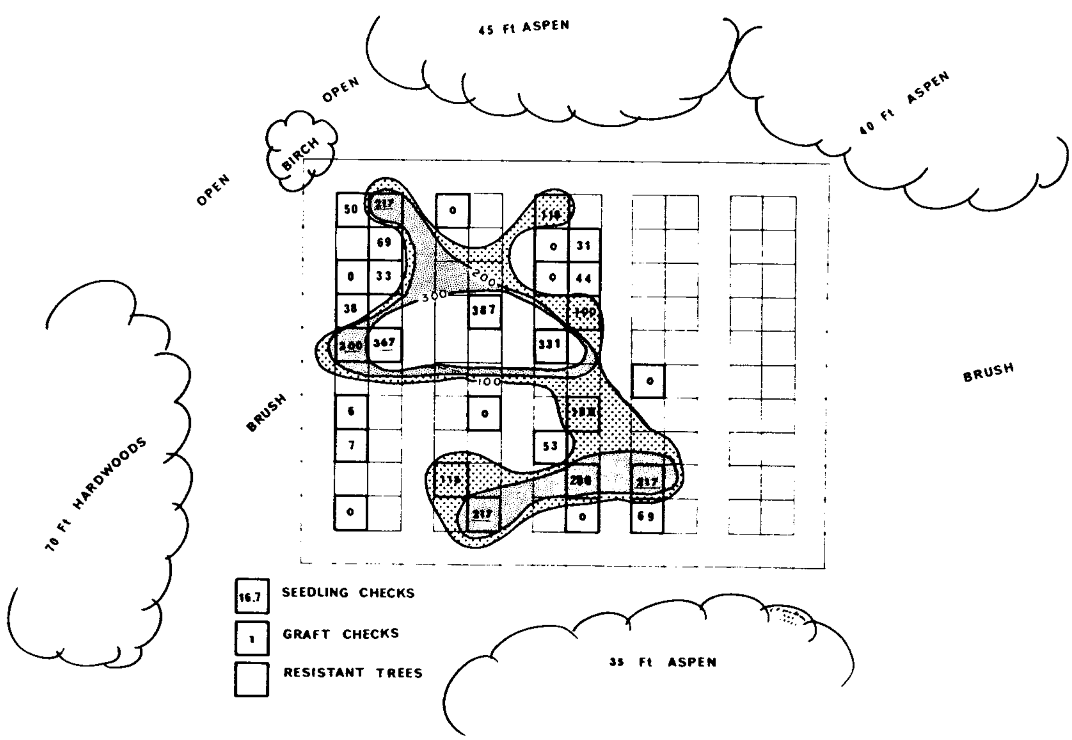

Figure 8. Numbers of blister rust cankers per 100 white pine seedlings (2-3 ft tall) in a forest opening at Whyte, Minn. Legend boxes show average infection rates. Graft check plot values have been multiplied by 16.7 to arrive at a corrected infection index for the graft canker plots.

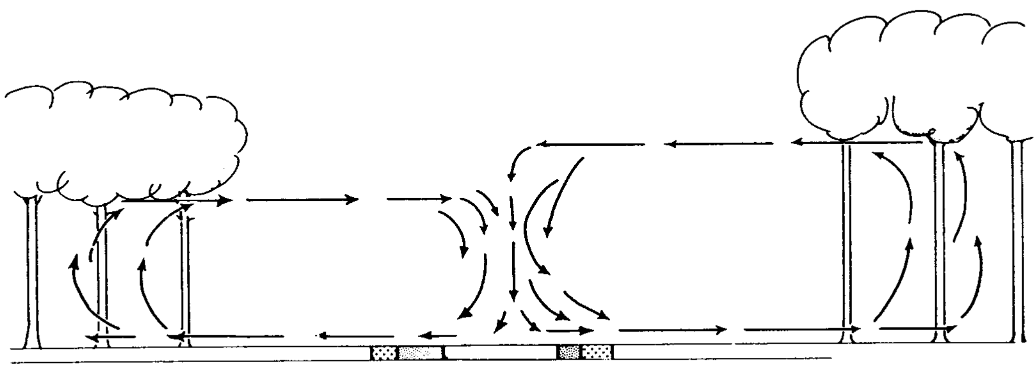

Figure 9. Diagram of an air circulation explaining the rust distribution in Fig. 8.

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.

BIOLOGY OF RUST RESISTANCE IN FOREST TREES:

PROCEEDINGS OF A NATO-IUFRO ADVANCED STUDY INSTITUTE

AUGUST 17-24, 1969

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.

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MISCELLANEOUS PUBLICATION NO. 1221

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

FOREST SERVICE
FEBRUARY 1972