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BLISTER RUST OF WESTERN WHITE PINE: RESEARCH STATUS NEED AND PROSPECTS FOR BRITISH COLUMBIA

by
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INTERNAL REPORT BC-39

DEPARTMENT OF THE ENVIRONMENT
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INTRODUCTION

Blister rust, caused by Cronartium ribicola J.C. Fischer, occurs on all five-needle pines, alternating on species of Ribes, was introduced into British Columbia early in this century. Spread throughout the range (36) of western white pine (Pinus monticola Dougl.), the main host in B.C., was rapid. Research on the disease and attempts to control it have been largely concentrated in the Inland Empire of the United States, which is located south of the host range in the interior of B.C. and where the host is especially abundant. In B.C., control of the rust by eradication of the alternate host was never considered feasible on account of the rugged terrain occupied by P. monticola. Some host resistance work was undertaken, which resulted in a small collection of resistant clones that now grow in the U.B.C. Forest at Haney, B.C.

The following report constitutes an evaluation of the blister rust situation in B.C. It presents a review of research on white pine blister rust, with emphasis on active programs involving western white pine. Early research was reviewed by Boyce (14) and Mielke (50). The feasibility of control of the rust in B.C. is discussed and the research programs considered necessary are outlined. To provide a clear understanding of the background on which the recommendations have been based, aspects of early research on P. monticola and other susceptible species judged especially pertinent to the choice of research routes are presented.

It is appreciated that the practical outlook adopted should be complemented, where research resources permit, by a program designed to improve understanding of as many fundamental aspects of the disease as possible. The history of attempts to deal with this disease does point to the dangers of large-scale control attempts started with an inadequate understanding of the factors involved. Risks are inherent in extrapolation of results obtained from small-scale research programs to the scale involved in control, but an understanding of the main mechanisms involved, together with a policy of small-scale developmental testing operated with adequate feedback for further research, should minimize these risks.

The report deals only incidentally with whitebark pine (P. albicaulis Engelm.) and limber pine (P. flexilis James), but they are highly susceptible. They occur largely as timberline or near timberline species, and whitebark pine occurs frequently in this situation throughout much of the mountainous area in southern B.C. The disease may be having important effects on these species, particularly in whitebark pine, but their importance is largely in watershed and recreational values even though P. albicaulis has been reported to form large trees occasionally in the Crows Nest Pass (24). The disease has been credited in the Pacific North West of the U.S. with reducing watershed and recreational values because of occurrence of the host on unstable soil situations and in places used for skiing (5).

Unless otherwise stated, all information for which no references are given was personally communicated by personnel at the U.S. Forest Service, Intermountain Forest and Range Experiment Station, Moscow, Idaho.

The author wishes to express his deep appreciation to U.S.F.S. personnel at Moscow engaged in blister rust research, and especially to C.D. Leaphart and R.T. Bingham. They were extremely helpful in making their extensive experience with this problem available to the author and providing free and frank information on trends in their recent studies.

The descriptions of their programs are necessarily brief and do not do justice to the programs themselves. The opinions expressed do not necessarily coincide with those expressed by the investigator concerned and the author takes full responsibility for his interpretations.

REVIEW

WESTERN WHITE PINE

OUTBREAK HISTORY

The early history of the epidemic caused by *C. ribicola* on western white pine in British Columbia has been well described by Lachmund (43). The rust was first discovered on western white pine (*Pinus monticola* Dougl.) in 1921 at several points in southwestern British Columbia and northwestern Washington. The infection was traced to a shipment of *P. strobus* plants brought from France in 1910 and planted at Point Grey. In 1922, the disease was found over most of the range of coastal pine in British Columbia. South of the border, it was found at Blaine and Mount Vernon. It was found in the interior of British Columbia at Canoe, Revelstoke and Beaton, apparently having been established there in 1917 as a result of favorable weather.

The most thorough description of damage in B.C. was obtained from plots established by Lachmund at Daisy Lake near Garibaldi (43), where infection had commenced in 1913. One plot, located under a canopy of alder and poplar, containing white pine regeneration up to 20 feet high, together with a high density of susceptible Ribes plants, constituted a natural disease garden. Over 90% of the trees had been killed by 1924 and by 1931, only one tree remained alive and it was heavily infected. In a second plot, located nearby but containing few Ribes plants, about 66% of the trees had been killed by 1931. On a third plot, located about 900 feet from a Ribes patch and containing some older trees, about 10% had died by 1924, all in the smaller age classes, and by 1931, only

11% of the trees had been killed, although 86% of the trees had infections.

Davidson (22) and Mielke (52) reported the damage that occurred on 500 3-year-old nursery seedlings planted in the Daisy Lake area in 1923. By 1929, all but 9 had been killed by the rust and by 1931, the remainder were infected.

The reports indicate that damage was highest in the Daisy Lake area, but damage in several other coastal areas of B.C. closely approached it. Putnam (64) reported results from northern Idaho that were also extremely severe. Near Revelstoke, plots established in 1929-30 showed that 3.4% of the trees were infected in 1922, but a wave year in 1927 produced a total of 34% infected (20). An extensive study in the Upper Arrow Forest in 1946 (17) showed that 76% of the white pine was infected by blister rust. An estimate of the mortality expected within different stands 15 years later gave projected mortalities varying from 14 to 87%.

CONTROL ATTEMPTS

Large expenditures were made, particularly during the 1930's and 1940's, in the western states of the U.S.A. in an attempt to protect western white pine and sugar pine by removing the alternate host, *Ribes spp.* (2,3). Control attempts by this method are based on evidence that basidiospores from Ribes plants rarely travel in a viable state beyond 1000 feet and usually travel much shorter distances (16, 52). Hand pulling and grubbing was employed in areas of high value. Later, herbicide treatments were employed (56). Recently, however, a survey of treated and untreated stands by Carlson and Toko (19) led to the conclusion that Ribes eradication is ineffective in reducing damage and the practice has been abandoned in the Inland Empire. The authors consider that long-distance transport of viable spores probably does occur, and that it explains the ineffectiveness of eradication in the many stands examined. Other possible explanations may involve failure to eradicate the Ribes even where retreatments were carried out. Stand clearing is believed to result in the germination of numerous Ribes seeds that have remained dormant within the duff for many years under the cool conditions provided by a closed forest canopy (25). The failure of Ribes eradication in western States as a control method contrasts with its effectiveness against this rust on eastern white pine in eastern Canada and the U.S. (13,29).

Extensive trials with antifungal antibiotics (55), involving both aerial and stem applications, were attempted to control the rust but were ineffective (46). There were indications that the antibiotics had enhanced the activities of the pathogen by killing a fungus, Tuberculina maxima, associated with canker inactivation.

RESISTANCE RESEARCH

An extensive program at the Intermountain Forest and Range Experiment Station under the leadership of R.T. Bingham is directed along several routes toward the efficient production of resistant stock, with the resistance in as stable a form as possible.

One route is directed toward the formation of seed orchards yielding seed with a substantial percentage of resistant progeny. This work is expected to provide approximately 9 million F2 seed, 50% resistant, by about 1985. At present, some F1 seed is being produced that yields approximately 30% of the seedlings capable of remaining disease-free after intense inoculation with the pathogen.

Studies to explore the occurrence of host resistance and its heritability commenced in the late 1940's (10). The selection of resistant "candidate" trees was commenced in high-hazard locations, controlled crosses were made, and the resulting seedlings were exposed to inoculum of the rust. Trees of general combining ability were recognized and the heritability of the resistance was studied (6, 11). Approximately 400 candidate trees were involved in the original selection program. A wide range of variation in the level of resistance transmitted to progeny was discovered among resistant trees (34). Only trees with high general combining ability for resistance in progeny were selected for seed orchard purposes. Later searches for candidate trees greatly enlarged the numbers available to provide as large a gene pool as possible for resistance. Mixed pollen crosses for appraising general combining ability (7) have been recently devised to hasten and reduce the cost of the testing process.

In a program terminated in 1960, Porter (61) selected western white pine with complete or almost complete freedom from blister rust symptoms in areas of severe infection. Grafts from the candidate trees were tested under severe infection conditions. One test of 14 trees, all of coastal origin, yielded 4 clones that were highly rated for resistance, while 4 others were considered moderately resistant. In a further test, 6 of 7 coastal trees were highly resistant, but only 1 out of 14 trees from the interior was resistant, and it was only moderately resistant.

Recently, resistance studies at Moscow have also proceeded toward a mass selection program in which seed from healthy trees in high hazard areas are used. Trees originating after commencement of the blister rust epidemic are preferred. If effective, the advantages of this technique are many, including lower cost, avoidance of a time delay in securing seed, and retention of a high degree of genetic heterogeneity. In its simplest form this concept would provide for use of natural areas as combined nurseries and disease gardens. Bingham has found, during the 20 years in which he has collected control seed lots from residual trees, that the level of survival in the control progenies has gradually improved. In recent tests, involving the use of very large amounts of inoculum, the level of "symptomless" seedlings was approximately 20%.

The application of this mass selection concept apparently had its origin (35) in a comparatively recent reorientation of the philosophy and tactics of plant breeding for disease resistance. This philosophy, as applied to agricultural crops, is presented by Van der Plank (68). Many of the studies underlying the new approach originated in Mexico, where experience with traditional breeding tactics applied to breeding of wheat varieties resistant to stem rust showed that the average commercial life of a variety was only four years before breakdown of resistance occurred on an epidemic scale (12).

The necessity for adopting the most stable forms of resistance possible for forestry purposes, with rotation periods many times longer than that for most agricultural crops, is obvious.

Mass selection techniques are expected to favor inclusion of stable types of resistance that might otherwise be omitted. The types of resistance believed to predominate in natural populations, where pathogen and host have co-existed for evolutionary long periods, are termed horizontal as distinguished from vertical types by earlier approaches to breeding for pathogen resistance. The vertical type is usually controlled by a single gene and is only effective against certain genotypes or races of the pathogen and would involve resistance to the races common in the country or region concerned. It usually has the advantage of immunity or near immunity. Horizontal resistance and tolerance reactions (the two may be indistinguishable in practice), in contrast, are believed to be polygenically controlled and effective against all races of the pathogen though accompanied by some tolerably low level of damage.

Studies of the resistance mechanisms in white pine and of their genetic control are making considerable progress at Moscow. Hoff and McDonald (35) have presented a summary of the various resistance reactions found. Evidence has accumulated that one resistant reaction, a needle spot mechanism, is controlled by two independent recessive genes (48). The presence of either one or both factors in a single plant resulted in needle spots involving only needle lesions. It has also been shown that a recessive gene controls a fungicidal reaction in the vicinity of the short shoot. In addition to the studies of resistant reactions and their inheritance pattern in *P. monticola*, studies are being undertaken on pine species regarded as naturally resistant to blister rust, including *P. armandi*, *P. griffithii*, *P. Koraiensis* and *P. sibirica*. Some earlier studies (34) involved interspecific hybrids between the native North American five-needle pines and those exotic species, with the hope of incorporating resistance into the native species. In one test, hybrids inherited the resistance of the parental *P. griffithii*. However, recent interest in the exotics lies in the contribution of knowledge on the most stable resistance mechanisms and in the hope that it will lead to improved tactics of utilizing natural variability.

The evolutionary origin of the resistance to blister rust in western white pine is unknown. However, evidence has accumulated (53) that suggests that this pine, or a very closely related ancestral form, probably had its origin in South East Asia, which Gaumann (26) considers the epicentre for the rust. Migration may have occurred over the land bridge across the Bering Straits that existed at one time, thereby providing a plausible explanation for the origin of this resistance evident in the candidate trees and their progeny. It is not known how host and fungus became separated but, whatever the explanation, the absence of the pathogen on this continent until this century would remove selection pressure for the resistance genes and could explain why so few members of the population were resistant when the pathogen was introduced.

HOST-PARASITE RELATIONS

Much effort has been directed toward an improved understanding of the physiology of the host-parasite relationship, and very substantial progress has been achieved.

The monocaryotic mycelium of the rust has been grown in pure culture (30,41), and direct cultivation on synthetic media is a real possibility. The fungus has also been grown, using an artificial membrane which acts as a molecular sieve interposed between the host and the rust (31). By varying the sieve structure employed, deductions have been made concerning the molecular size of the metabolites required by the rust from the host. Recent work (32) has shown that nonhost cultures of Douglas-fir attracted the rust and permitted haustorial formation. It is hoped to obtain single spore lines of the rust in future.

The ability to culture the fungus will be a powerful tool for determining the influence of a variety of biological and other agents on the rust. Direct culturing could facilitate a screening program designed to select systemic fungicides which, if promising, would lead to tests for field effectiveness.

Research is also being conducted on the influence of infection on metabolic pathways and enzymatic changes in pathogenesis. Data indicate that infection disrupts the normal pattern of movement to metabolic sinks in a way that differs with the element concerned. Calcium was accumulated in host tissue adjacent to canker tissue, whereas potassium, magnesium and phosphorus all concentrated in the sporulative area of cankers, and sodium concentrated in canker margins. The interaction of host phenolics with cellulases and pectinases also is under investigation. These enzymes have been found to play an essential role in entry of the pathogen, and evidence suggests that glycosidal formation may be involved in detoxification of the phenolics. It is hoped that understanding the metabolic sequences involved in canker formation and the subsequent exchange of metabolites will assist in selecting those fungicides most likely to be translocated to the rust.

BIOLOGICAL CONTROL RESEARCH

Another line of research being conducted at Moscow is directed toward biological control. In this context, biological control refers to the influence of organisms other than man, not necessarily introduced deliberately, on the level of damage caused by the pathogen. Studies have concerned the range of organisms, chiefly fungi, occurring on rust cankers, and a screening of them as potential control agents. However, experimental studies of effectiveness against the rust have involved only one of these fungi, Tuberculina maxima. Inoculations, using culture mycelium, have demonstrated its capacity to inactivate cankers (73), although observations were not continued long enough in the study concerned to determine if reactivation occurred.

Wicker (72) reported that canker invasion by T. maxima resulted in digestion of the host cells, which is in agreement with results by Lechmere (47) and indicates that it does not function as a hyperparasite on the rust. Wicker was able to infect in vitro cultures of rust-free callus tissue of western white pine. However, he also reported that T. maxima ceased invasion at the margins of the rust canker.

Powell (62,63) recently reported on the occurrence of T. maxima on various rusts in western Canada. It has been collected from many locations in British Columbia and southwest Alberta. Powell speculates that it is probably more widespread than the collections indicate. There are no reports of it on whitebark pine or limber pine in Canada or the U.S.

A survey of inactivation of blister rust cankers throughout the Inland Empire in 1965 (39) showed that 62% of the cankers were inactive. For the purposes of this study, the cause of inactivation was ignored. No cankers less than 4 years old were completely inactive, but 50% were completely inactive at 8 years and 90% at 24 years. This age relationship may, in large part, reflect the period of exposure and hence the probability of contact with inoculum. Kimmey (37), whose experience with T. maxima on blister rust in the areas went back for many years, suggested that T. maxima was found only rarely on cankers 30 years before the survey. He stated that T. maxima, now common in the area, was believed to be the principal cause of the inactivation but that other causes undoubtedly exist. Comparison of his results with those in a survey by Bingham and Ehrlich (8) from the same general area published in 1943 also suggests that canker inactivation has become much more frequent in recent years.

Other associated studies being conducted at Moscow involve attempts to use infra-red sensing techniques as a quick method to determine viability of cankers. The method is based on detection of an increased respiration rate associated with active canker development. At present, the only method available consists of repeated observations over a period of years.

SILVICULTURAL CONTROL RESEARCH

The possibilities for silvicultural control of blister rust have been of interest for a considerable time and continue to attract research. A paper by Moss and Wellner (54), issued in 1953, described a wide variety of measures designed to hinder the establishment and growth of Ribes plants. The Ribes species of the Inland Empire are said to establish themselves in full sun or lightly shaded sites after fires, logging or other major disturbances to forest cover and forest soil. Control recommendations emphasized burning off of humus to reduce the Ribes seed supply and the use of selective logging to maintain more than 50% shade, a condition claimed to produce a high mortality in the Ribes seedlings. Unfortunately the information and suggestions cannot be evaluated critically because of the absence of details of methodology and results of experimentation. Current opinion apparently regards the overall concept as valid, but impractical.

Another approach to control being investigated at Moscow concerns the effectiveness of various silvicultural treatments, especially thinning and pruning. At 15 years of age, the average stand in the Inland Empire has approximately 47% of the stems infected and about 89% of these result in tree mortality. Data from surveys indicate that 98% of the infections are lethal in trees at 6-10 years of age, 73% at 16-20 years, 41% at 26-30, and 34% at 36-40. However, it is not clear whether this data takes canker inactivation into account. Thinning at about 15 years is estimated to permit removal of most of the trees with lethal cankers and to ensure optimum growth of the remaining trees for 10 years or more. The enhanced growth resulting from thinning, and perhaps fertilization, is also likely to produce trees with sufficient branch growth to greatly reduce the hazard to cankers being lethal. Some branch internodes are too long for the fungus to traverse after girdling and the fungus dies without reaching the main stem. Data from plots in the Inland Empire region indicate that annual terminal branch increments on open-grown trees for the first two growth segments from the bole average distances greater than cankers can successfully cross. Studies are also being conducted on the application of pruning. Their data suggest that 70% of the lethal infections initiated during the first 20-30 years of growth occur in a prunable zone up to 17 feet above ground.

EASTERN WHITE PINE

The disease has been reported on all the five-needle pines, but the susceptibility of different species varies considerably and the Asiatic species are generally believed to be the most resistant. However, for historic and geographic reasons, much of the information on the rust has been obtained from studies on the canker produced on eastern white pine (Pinus strobus L.).

Eastern white pine was introduced into Europe in 1705 from North America and it was planted extensively. The rust was not discovered on it until nearly 150 years later (74) and it was not until 1904 that Klebahn (40) experimentally proved the connection with the disease on Ribes that led to the use of the name C. ribicola for the disease on pine. Cronartium ribicola is generally believed to be an asiatic species (26) and the 150-year gap is interpreted as evidence that the rust was not native to Europe. The large-scale plantings of P. strobus in Europe, coupled with the widespread use of black currants, a most susceptible species, led to an epidemic throughout the main areas where this pine had been planted (58). As a result, in Europe, the planting of P. strobus in forest stands has been almost entirely discontinued.

Cronartium ribicola was first discovered in North America at Geneva, New York in 1906, when it was found on Ribes. It was discovered on P. strobus in 1909 (14). Later, it was deduced to have been introduced on young plants of P. strobus in 1898 or a few years earlier, from a German nursery. Millions of the small trees, many of them infected, were brought in from Europe between 1907 and 1909 and planted throughout the Northeastern States, the Lake States and eastern Canada (14). Damage was great wherever susceptible Ribes plants occurred in substantial numbers.

Ribes eradication has, however, proved effective in many areas (29,60). Damage in nurseries has been controlled by this eradication policy

(13). In Ontario, a survey of plantations (18) showed that young plantations of pure white pine effectively shaded out any Ribes plants that had become established following logging or fire. Damage in Ontario was severe only where plantations occurred next to natural hardwood stands, where Ribes tend to occur, or in older plantations where management practices encouraged opening of the crown canopy for extended periods.

Attempts to select and breed resistant eastern white pine commenced at Wisconsin in 1937 (65). Screening of grafted material under conditions more or less optimum for infection, together with infection tests on progeny from selected crosses, led to selections that showed transmission of resistance to some of the progeny. In addition, many interspecies crosses were made involving _P. strobus_ and species considered to be relatively low in susceptibility (57). Crosses with _P. griffithii_ resulted in the highest percentages of resistant progeny, but they were more susceptible to winter injury. Although much was learned about resistance and its inheritance, the work does not appear to have led to any large-scale developments.

Heimburger (33), in Ontario, involved for many years in a selection program for resistant eastern white pines and studies of inheritance, concluded that resistance in this host is inherited in a polygenic manner. Surveying the work on _P. monticola_ up to 1962, Heimburger considered that resistance in _P. monticola_ appeared to be less polygenic than in _P. strobus_.

In the lake states, E.P. Van Arsdel developed a climatic hazard map (68,69). No rust was found in the warmest part of Wisconsin, whereas progressively cooler and wetter regions had increasing numbers of rust infections. One zone had rust only when wild Ribes bushes were very close to the pines. Van Arsdel (67) also studied patterns of spore dispersal by tracing smoke movement from Ribes-infested swamps, and used this to explain infection gradients. In this way, the factors underlying some high-hazard conditions were explained.

RESEARCH REQUIREMENTS AND RECOMMENDATIONS FOR BRITISH COLUMBIA

INTERIOR RESEARCH REQUIREMENTS

A distinction is drawn between the coastal and interior situation for several reasons. The major reason is that whereas the host continues to reproduce itself readily and to occupy large areas of land throughout the interior wet belt, it now occupies relatively little land at the coast. The value of a research program on blister rust in coastal areas must be based primarily on the advantages anticipated from replacing other tree species by western white pine.

It is recommended that a research program be carried out within the natural range of *P. monticola* in the interior, designed to eventually permit white pine management with acceptable and predictable levels of losses in these stands. This recommendation is based on a consideration of several factors, including: the many desirable characteristics of *P. monticola* from ecological, silvicultural and wood value standpoints; the continuing occupation of land by *P. monticola*, even where disease incidences are high; the actual damage caused by blister rust and its potential for destructiveness, and the value of maintaining species diversity in a world of rapidly changing conditions.

Western white pine, apart from its susceptibility to blister rust, is a highly regarded tree from various standpoints. In the mountains of northern Idaho, where conditions are probably similar to those in much of southern B.C., Larsen (45) found it occupying slopes at elevations of from 2500 - 5000 feet. White pine maintained a relatively rapid rate of height growth and, in most situations, overtopped competing species. Its characteristic of retaining viable seed buried deep in the duff, which germinate upon removal of the overhead canopy, has ensured a supply of seed subsequent to most fires (25).

The continuing occupation of land by *P. monticola* constitutes an important factor in considering the need for research on blister rust in the interior. Rowe (66) states that *P. monticola* occurs in the Northern and Southern Columbia sections, but disappears in the northwestern and northern parts of his Northern section. The author encountered extensive areas occupied by *P. monticola* throughout what is known as the interior wet belt. The host comprised a high proportion of trees in many stands but, in others the additional species present, chiefly western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn) and western larch (*Larix occidentalis* Nutt.), predominated. Even in locations where losses from blister rust appeared to be high, *P. monticola* reached cone-bearing age in sufficient numbers to ensure a continuing supply of seed. Thus, any attempt to treat *P. monticola* as a weed species and eliminate it would be very costly. Subsequent treatment to ensure adequate stocking by alternative species would be necessary in many areas, and would also contribute to costs.

The damage caused by blister rust during the early phases of the epidemic has been well documented. It illustrates the potential for disastrous damage when this pathogen is in contact with a largely susceptible host population growing under environmental conditions favorable to the pathogen.

A study of damage caused by blister rust in the Upper Arrow Forest was carried out in 1946 by Buckland (17). This survey showed that between 47.6% and 92.7% of the white pines were attacked. Childs and Kimmey (20) reported the following levels of infection in plots near Revelstoke: 7% of trees 0.1-5 feet high; 23% of trees 5.1-10 feet high, and 79% of the trees 35.1-40 feet high. Several factors influence the likelihood of an infection causing tree mortality but, nevertheless, these figures illustrate the fact that damage caused by the rust in the interior is substantial. The author's observations substantiate this, although considerable variation was found.

The final point to be made in favor of research on blister rust in the interior is the insurance value of retaining the species for forest management purposes in a world of rapidly changing conditions. The spread of blister rust is a classic example of the potential destructiveness of a pathogen when removed from its native environment. The spread of the larch casebearer, Coleophora laricella (Hubner), into the southern interior of B.C. (23) constitutes the second major invasion of an exotic pest there during this century. The likelihood of further introductions is increasing as world travel expands.

INTERIOR RESEARCH RECOMMENDATIONS

Three main lines of investigation appear to offer substantial hope of leading to control techniques in the interior of B.C., and it is recommended that such research be pursued. They are investigation of the value of employing tree cover over Ribes along stream banks; investigation of the major factors responsible for the great variation in incidence of the disease in different stands, and investigation of the possibilities for augmenting the level of canker inactivation.

Observations by the author suggest that Ribes plants in the West Kootenays tend to occur at altitudes of 5000 feet and higher, or to be concentrated along stream banks at much lower elevations. Retention of tree cover along these streams at harvesting should minimize the significance of the Ribes there as suppliers of inoculum to any nearby regeneration by filtering aeciospores before they reach the Ribes and basidiospores before they reach white pines. Studies are required to verify these observations and to determine the distances involved for effectiveness. The work in Ontario (18), which indicated that plantations of white pine effectively shaded out any Ribes plants, provides some evidence of capacity of tree cover to restrict development of Ribes plants and influence the risk of infection. Moss and Wellner (54) make claims similar to those from Ontario. Assuming the technique proves of value, information on Ribes occurrence in relation to stream banks will be required for all areas.

It is also recommended that an inquiry determine the major factors responsible for variations in disease incidence that occur. Until the major factors influencing variation in incidence are understood there can be no prediction of incidences likely to occur in successive rotations or of repetition of existing incidences. An understanding of these factors would also facilitate construction of a blister rust hazard map. Buckland (17) found that the percentages of pine attacked by the rust ranged from 48 to 93. The author obtained percentages varying from 2 to 46 but, unlike Bucklands study, this was obtained primarily, though not exclusively, in regeneration which constitutes a smaller target for inoculum, and different areas, with only a slight overlap, were sampled.

The factor or factors responsible for the variation in incidence is unknown, but inoculum levels and climatic variation appear to warrant investigation. Inoculum concentration is a function of a number of factors, but some likely to be important include Ribes densities, susceptibility of the Ribes species involved, their proximity to white pines, and the degree of cover provided by non-susceptible tree species. Analyses of weather records from several stations in the area may demonstrate whether or not intra-regional climatic variation is likely to be a major variable influencing the infection process.

A further recommendation for study concerns canker inactivation. Field data are required on frequencies of permanent canker inactivation in B.C., irrespective of the cause of inactivation. This information can only be obtained by repeated observation of individual cankers for several years. Data from one location are available for analysis. These data were collected over five years in the course of antibiotic spray trials against blister rust conducted by the B.C. Forest Service (Glew, personal communication). It involved repeated measurement and drawing of canker development. The position of sporulating material of T. maxima was recorded.

Studies have attributed canker inactivation to T. maxima (39, 72), but the published data were obtained by observations that could not preclude the possibility of canker reactivation. The inability to determine the viability of rust mycelium in cankers judged inactive has constituted a major difficulty. Furthermore, strains of T. maxima may exist that affect the process of inactivation differently. However, analysis of repeated measurements of cankers, carried out over six years, is in progress at Moscow, and decisions regarding studies of the causation of canker inactivation will have to await the results of this analysis.

One aspect of the influence of *T. maxima* on blister rust that requires study in B.C. concerns its activity in suppressing aeciospore formation within stands. This suppression accompanies canker inactivation, regardless of possible canker reactivation at a later time. Observations by the author suggests that *T. maxima* can often form high incidences within regeneration and that this results in few aeciospores being produced. Information is required on the distribution of *T. maxima* within the area occupied by *P. monticola* and on its spread within stands, as this is likely to have an influence on the likelihood of new rust infections becoming established.

COASTAL RESEARCH

It is recommended that the potential value of *P. monticola* to coastal forestry be evaluated by qualified individuals before reaching a decision as to whether or not a coastal research program on the rust should be initiated. Most of the reasons given for concluding that research is required in the interior also apply at the coast, but the relatively small areas occupied by *P. monticola* at the coast today excludes the major one.

The following discussion of the prospects for control and associated research is provided to assist in deciding on the level and probable duration of support for a coastal blister rust research program (on the assumption of a sufficiently favorable evaluation of the host species).

It is recommended that top priority in any coastal research program into this disease be accorded to testing and developing a mass selection program for resistance. Careful consideration should also be given to the possibility of cooperating with another agency or agencies in developing a seed-orchard program that would supply seed yielding resistant progeny.

The history of the early stages of the epidemic, together with some observations of damage made by the author at the coast, suggests that, with the possible exception of a few locations on Vancouver Island, the entire coastal zone is subject to a high hazard of infection. Under high-hazard conditions, the use of host resistance offers the best hope for growing the host with a low level of damage. The early studies of Porter (61) and subsequent experience with the resistant clones demonstrate that individual resistant plants can be grown with a low level of loss at the coast. Similarly, the studies conducted by Bingham and his group establish this for conditions in the Inland Empire. However, the subsequent stability of resistance when large-scale plantations are well established is impossible to predict with certainty, although evidence is available.

Of the possible methods for obtaining resistant stock, the mass selection approach is most likely to yield stable resistance and should receive priority in a research program. The existence of several resistant mechanisms (34,35,48) in P. monticola, the evidence from the Moscow group that tolerance mechanisms exist in the host and recent advances in agricultural methods for ensuring resistance stability provide substantial grounds for long-term optimism on the prospects for this approach. However, its use involves many assumptions that must be tested and practical problems may arise to delay the success of the work. In view of the paucity of information available, it is not possible to predict when practical methods may be expected.

Because of the extent of untested assumptions involved in developing the mass selection approach and the likelihood, in the author's opinion, of a substantial delay before it can be utilized on a practical scale, the seed-orchard approach might be utilized for an interim period. The techniques involved have been well explored by the Moscow group. A small nucleus of resistant clones for seed-orchard use was provided by the work of Porter (61). Tests for general combining ability would be required before they were used in any program. The numbers of clones should be increased as soon as possible, preferably by a further search for candidate trees in B.C., followed by screening for resistance under disease garden conditions. However, it might be possible to obtain suitable clones from the U.S. program as part of a cooperative program of clonal testing. The main objection to use of a seed-orchard program lies in the restricted genetic variability anticipated with it. However, assuming thorough initial testing of resistance, the dangers of instability are theoretical ones based on analogy with agricultural experience. The analogy is not a perfect one and, unfortunately, there is no known method for testing it critically on a small scale. The fact that the Moscow program commenced with a seed-orchard approach and has now added the mass selection approach to its research program is evidence of concern on their part, but the seed-orchard program is nevertheless being maintained.

SUMMARY

This report examines the need for research on blister rust of

Pinus monticola in British Columbia and recommends a program for the interior. It also recommends that the potential value to coastal forestry be assessed before deciding on a research program for the coast.

Research on blister rust is reviewed. Research proposals for the interior involve three topics that hold promise of practical application in controlling the rust. The first concerns the occurrence of differences in the levels of damage in different locations. The second concerns distribution of the alternate host, *Ribes* spp., along streams and the possible value of retaining tree cover. The third topic involves canker inactivation.

In the coastal situation, a research program, if initiated, should give priority to developing a mass-selection approach for host resistance, although the seed-orchard approach may have interim value.

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