



REVIEW

Silvicultural management of white pines in western North America

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Summary

Since the introduction prior to 1915 of white pine blister rust (*Cronartium ribicola*) into the forests of western North America, many populations of native white pine species have seriously declined. Because western white pine (*Pinus monticola*) and sugar pine (*P. lambertiana*) are highly valued timber species, their silviculture under intensive management is well-documented. The silviculture of other white pine species has received less attention but is no less important. For all western species, silvicultural management is a key component for sustaining and restoring viable white pine populations. This review examines approaches for assessing and reducing blister rust hazard, regenerating white pine stands, and tending established stands to reduce damage and impact from blister rust. Hazard and risk ratings provide means for assessing the potential severity of blister rust infestation and its probable impacts on management. An epidemiological simulation model is available for describing complex pathosystem interactions, their consequences on white pine growth and survival, and likely outcomes of silvicultural activities. Until the 1960s, *Ribes* eradication was the principal method for blister rust control; it is now rarely used except for high-value trees. The choices of harvest and site preparation methods are critical for successful white pine regeneration. As host responses to blister rust infection are inherited, regeneration is an opportunity to increase seedling survival and disease resistance. For artificial regeneration, the western genetics programmes provide improved planting stock. For natural regeneration, the selection and retention of well-adapted white pines as seed sources can enhance stand genetics. Thinning and pruning are common silvicultural activities for tending stands and are readily modified for blister rust-infested stands. Although biological and chemical agents have been used, their performance has been less than satisfactory. Likewise, genetics and other silvicultural practices have also demonstrated limited success in blister rust control. An alternative, adaptive approach could use both silvicultural and genetic techniques to mitigate impacts and maintain white pines.

1 Introduction

In less than a century after introduction of *Cronartium ribicola* J.C. Fisch. in Rabh., causal agent of white pine blister rust, populations of western white pine (*Pinus monticola* Dougl. ex D. Don), sugar pine (*Pinus lambertiana* Dougl.), whitebark pine (*Pinus albicaulis* Engelm.), and several other species have seriously declined. The number of western white pine trees has decreased 90% in northern Idaho, and the species has been reduced to a minor component in stands it had historically dominated (NEUENSCHWANDER et al. 1999). Impacts of blister rust are so severe and widespread that several white pine species of western North America are no longer commercially significant. Replanting is curtailed by a fear that seedlings will not survive to maturity. Where species survival for biodiversity is desired, white pine may be maintained by protective use of silviculture.

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1.1 Western white pine

In the western region of its distribution, western white pine grows from sea level to approximately 1200 m near Knight Inlet in British Columbia, progressing upward in elevation as it continues south along the Coast, Cascade (350–1450 m), Siskiyou (1830–2140 m), and Sierra Nevada (1830–2300 m) mountain ranges to Tulare County, California (TOMBACK and ACHUFF 2010). In wetter areas, the distribution extends from Quesnel Lake south along the interior mountain ranges of British Columbia into eastern Washington, northern Idaho and western Montana until gradually diminishing to a southern limit in the Blue Mountains of eastern Oregon (GRAHAM 1990; KLINKA et al. 2000). Within this Inland Northwest region, the species ranges from 500- to 1800-m elevation. Western white pine no longer dominates forest stands as it did a century ago. It persists as only a minor component (NEUENSCHWANDER et al. 1999) in stands converted to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western larch (*Larix occidentalis* Nut.).

There are four reasons why western white pine is still well-regarded as a commercial species in western North America. First, it is a very productive and desirable tree owing to rapid growth, a clean bole with minimum taper, narrow crown, and non-resinous wood (KLINKA et al. 2000). On many suitable sites, western white pine matches or exceeds the productivity of other commercial species, including Douglas-fir, a species with which it shares considerable similarity in range and growth habit (BISHAW et al. 2003). Second, western white pine has a genetic plasticity that allows seed transfer across large gradients in latitude and elevation (MEAGHER and HUNT 1999; KING et al. 2010). Third, although the supply has considerably declined over the last half century, western white pine still commands premium stumpage and milled values owing to its wood quality and desirability in wood remanufacturing (HOWARD 2001). Finally, western white pine has low susceptibility to laminated root rot (*Phellinus sulphureus* (Pilát), syn. *P. weirii* (Murr.) Gilb.), a root disease often fatal to Douglas-fir (THIES and STURROCK 1995).

1.2 Sugar pine

Sugar pine is the largest of North American pines and is the most widely distributed white pine in California. Its distribution extends from Clackamas County, Oregon in the Cascade Range south through the Siskiyou, Klamath Mountains, and Sierra Nevada, ending in the Sierra San Pedro Martir of Baja California (GRIFFIN and CRITCHFIELD 1972; TOMBACK and ACHUFF 2010). Sugar pine does not occur in single-species stands but typically comprises 5–25% of mixed conifer stands (HARLOW and HARRAR 1958) with ponderosa pine (*P. ponderosa* Dougl. ex Laws.), Jeffrey pine (*P. jeffreyi* Grev. and Balf.), red fir (*Abies magnifica* A. Murr.), white fir (*A. concolor* (Gord. and Glend.) Lindl. ex Hildebr.), Douglas-fir, giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), California black oak (*Quercus kelloggii* Newb.), and tanoak (*Lithocarpus densiflorus* (Hook. and Arn.) Rehd.).

Eighty percent of sugar pine volume is on public lands in California (AHLSTROM 1996). Its great size, straight bole, and distinctive wood characteristics make sugar pine one of the most valuable pine species. Extensive harvesting of sugar pine began during the California Gold Rush of 1849 and continued until recently (CERMAK 1996). A sugar pine infected by *C. ribicola* was first discovered in 1927 near the Rogue River in southwestern Oregon (MIELKE 1938); and blister rust was established in northern California by the 1930s. Blister rust has since continued to spread to the southern limits of the Sierra Nevada but has not been reported south of the Tehachapi Mountains (SCHWANDT et al. 2010).

1.3 Other white pines

The white pine species native to western North America other than western white pine and sugar pine occur principally at high elevations (TOMBACK and ACHUFF 2010). These other species have limited timber value and have not been managed on the scale and intensity applied to western white pine and sugar pine. Very little published literature describes the treatment history or reviews the silviculture of these other white pines for control and mitigation of *C. ribicola*. What does exist (see GEILS et al. 2010) mainly refers to whitebark pine, limber pine (*Pinus flexilis* James), and southwestern white pine (*P. flexilis* James var. *reflexa* Engelm. syn. *P. strobiformis* Engelm.). SCHWANDT et al. (2010) provide a detailed account of the extent and effects of blister rust on these white pine species.

This review summarizes past and present cultural, biological, and chemical practices used with variable effectiveness to control blister rust, limit its damage, and mitigate its impacts in white pine ecosystems of western North America. This review is divided into three sections covering assessment and reduction of site hazard, regeneration, and stand tending activities.

2 Assessing and reducing hazard and risk

2.1 Hazard and risk rating

In common usage, the terms hazard and risk, respectively, refer to a 'source of danger' and a 'possibility of loss'. Although hazard and risk are variously defined in the literature, a clear distinction between the two concepts and a consistent application of terms provide a logical basis for discussing *C. ribicola*. STILLINGER (1944) used hazard for 'the favorableness of the particular site for the development of the [white pine blister] rust'. The three key points conveyed by hazard as a source of danger from blister rust are: (1) a situation in space and time; (2) driven by environmental factors of climate and host distributions; and (3) a relative indication of the likelihood and severity of infestation (see McDONALD et al. 1991). A site that is well-removed from inoculum sources and rarely cool and wet enough for infection presents a low hazard. If white pines are present, then a few might become infected; but an infestation with many infected trees would be unlikely. Risk fundamentally refers to a probability of an undesirable outcome (see MADDEN et al. 2007). In our application, risk adds the idea that resource values or management investments are at jeopardy because damage resulting from blister rust infection reduces host growth, reproduction, and survival sufficiently to impact economic or ecological objectives. Planting might increase an investment risk over that of natural regeneration, but judicious use of resistant seedlings could reduce the risk of regeneration failure.

Relationships of the likelihood and severity of infestation to various environmental factors have been examined for western white pine, sugar pine, and other western species (see OSTRY et al. 2010, for discussion related to eastern white pine, *P. strobus*). Incidence is often used to determine site hazard, but the percent of trees infected or cankered (a physical manifestation of being infected) has several limitations as an indicator of hazard. Incidence is a useful measure for stands with a single or few cankers per tree, but severity (any statistic for infection density) is more appropriate where a host has numerous infections (SEEM 1984). For severely infested western white pine in northern Idaho, McDONALD et al. (1981) proposed a *rust index* defined as the cumulative number of cankers per thousand needles per year (also see HAGLE et al. 1989; CATLIN et al. 1994). As a stand develops, it is exposed to multiple infection events, trees grow and die, and cankered branches disappear; so, incidence and severity change over time even if the environmental conditions underlying hazard have not. Although information on the factors that directly control inoculum production, dispersal, and infection are seldom available, surrogate

variables describing climate, past weather, landscape features, site physiography, and vegetation can usually be obtained and used to characterize hazard.

2.1.1 *Western white pine*

The range of western white pine falls within a climatic zone that is typically favourable for blister rust development, but other environmental factors can influence the severity of infestation on particular sites. HUNT (1983) found that hazard for interior British Columbia was generally low when compared with northern Idaho and where the hazard on slopes was greater than on flat sites. RUST (1988) developed an expert system for northern Idaho to assess the blister rust hazard related to site factors affecting *Ribes* abundance. A study by MULLER (2002) and reported by SCHWANDT and FERGUSON (2003) correlated blister rust incidence with plantation-level variables of slope, elevation, and latitude and with plot-level variables of presence of *Ribes*, habitat type, brush height, and site preparation method. For 66 plantations reported by SCHWANDT and FERGUSON (2003), rust severity (cankers per tree) and mortality (percent dead) were highly correlated with stand incidence. Differences in incidence were significant for several comparisons; for example, mean incidence was nearly double (40 *vs.* 22%) for plots with *Ribes* than for plots without *Ribes*.

2.1.2 *Sugar pine*

The distribution of sugar pine extends across northern and southern climatic divisions that differ significantly in annual precipitation. Its ecological range spans from canyon bottoms to ridge tops within a mid-elevation, montane zone where *Ribes* are generally widespread and abundant (QUICK 1954, 1962a). The continued absence of blister rust in southern California several decades after *C. ribicola* had spread throughout the Sierra Nevada (KLIEJUNAS 1984; DENITTO 1987) suggests an arid climate is responsible for that region's low hazard. Further north (including the Sierra Nevada), however, the climate is sufficiently variable so that occasional summer rains are sufficient to allow spread.

On a landscape scale, variation in site attributes and *Ribes* associations complicate hazard assessment. Site attributes related to blister rust hazard include canyon physiography and topographic position (QUICK 1962a; KLIEJUNAS 1984). The susceptibility of *R. roezlii* Regel varies geographically; where it is severely infested, it readily defoliates and thus contributes little inoculum. *Ribes nevadense* Kellogg is less susceptible but retains infected leaves; so, it still contributes inoculum, especially when associated with *R. roezlii* (KIMMEY and WAGENER 1961; ZAMBINO 2010). Low-hazard regions and sites can be identified and expected to support no or very few infections. Within infested landscapes, high-hazard sites can be identified; most susceptible sugar pine trees are expected to become infected. Moderate-hazard sites are those where incidence is least predictable because the annual infection rate is so variable.

2.1.3 *Other white pine species*

Other species of white pine range from high-elevation, alpine communities to lower-elevation, montane forests on sites of low to high hazard. Most sites in the northwestern portion of the whitebark pine distribution have an environment generally favourable for blister rust and infestations are usually severe. In contrast, hazard is low at the southern extremes of the distribution; and blister rust is uncommon or absent. Even within British Columbia where incidence was too variable to relate to geographic attributes, ZEGLEN (2002) found a trend of increasing incidence from west to east across the province for whitebark pine.

White pine blister rust incidence was also highly variable across the greater Yellowstone area (northwestern Wyoming and adjacent areas), the central Rocky Mountains (southern Idaho, western Wyoming), and the southern Rocky Mountains (central Wyoming and Colorado). Yellowstone sites with low hazard were attributed by HENDRICKSON (1970) to the cold, dry environment for whitebark pine and limber pine and were related by NEWCOMB (2003) to the distance of whitebark pine from the habitat of *Ribes hudsonianum* var. *petiolare* (Dougl.) Jancz. SMITH and HOFFMAN (2001) modelled incidence of blister rust on both whitebark pine and limber pine to numerous site and vegetation characteristics for the central Rocky Mountain region. Their significant predictors included elevation, tree diameter, summer precipitation, presence of *Ribes*, stand density, topographic position, and percent slope. Their models correctly classified stands as having low (<25%), moderate (26–50%), or high (>50%) incidence in 62–76% of cases. KEARNS (2005) related incidence of blister rust on limber pine to a set of variables describing site characteristics, local climate, landscape-level abundance of *Ribes*, and infestation age. The analyses also described the distributions of *Ribes* (KEARNS et al. 2008) and projected blister rust hazard throughout Colorado—most of which was not yet infested.

Cronartium ribicola has only infested southwestern white pine in New Mexico since 1969 (FRANK et al. 2008) and several other locations in the Southwest (including Arizona) within the past several decades (SCHWANDT et al. 2010). In this region, southwestern white pine occupies numerous isolated mountain ranges (sky islands), each with a different weather pattern (arrival and amount of summer rains) and distinct *Ribes* flora and abundance (absent in some ranges). At a broad scale extending into Nevada, Utah, and Colorado, FRANK et al. (2008) developed a synoptic weather model estimating the relative likelihood of blister rust spread and intensification from white pine to *Ribes*. The model suggested a moderate to high hazard for some Southwestern mountains and low to moderate for other ranges. At a landscape scale, GEILS et al. (1999) proposed and tested a preliminary hazard model for the Sacramento Mountains, New Mexico using elevation, plant association, and topographic position. CONKLIN (2004) monitored 14 sites in the Sacramento Mountains for >10 years, including three sites not initially infested; blister rust incidence increased over time and the rate of increase was steeper for higher elevation sites.

2.2 Epidemiological simulation

A hazard model characterizes the environmental potential for blister rust infestation for an area; an epidemiological model describes the expected development of *C. ribicola* within a white pine stand. McDONALD et al. (1981) constructed a computer program to simulate infection of individual trees, disease consequences to tree growth and survival, and effects of silvicultural treatment. Blister rust functions of this model project infection, canker development, sporulation, and spread using the rust index, weather data, site variables, and host information for both pine and *Ribes* (FOREST HEALTH TECHNOLOGY ENTERPRISE TEAM 2007). Functions to project tree growth and survival and to simulate silvicultural treatment are provided by a base growth and yield model (DIXON 2002). The combined Blister Rust-Forest Vegetation Simulator (BR-FVS) is a complex computer program that uses numerous observed relationships and generates a series of tables enumerating changes in tree density by size and condition classes.

The BR-FVS is a practical tool for assessing expected outcomes of various silvicultural options, but several cautions are warranted. The blister rust model (McDONALD et al. 1981) links numerous epidemiological functions that may be individually known, but their interactions in a complex system are not well-understood owing to feedback and over-specification. Although many of the BR-FVS functions have a stochastic component, a single simulation presents only one expected outcome; bootstrapping multiple simulations reduces the uncertainty associated with a scenario (GREGG and HUMMEL 2002).

MCCLELLAN and BILES (2003) found bias in one FVS variant which underestimated tree growth compared with their reference stands. Although growth and yield functions can be calibrated to adjust from regional averages to a local stand, the data used to develop these functions are historical, reflecting tree performance in a past climate. White pines are genetically adaptable within a relatively wide climatic range (MEAGHER and HUNT 1999); so, a climate-sensitive, growth and yield model (FVS) could still remain a practical tool for assessing silvicultural options. Blister rust epidemiology is especially complex and contingent on many factors, such as weather. Although climate-rust models could be informative, a high level of long-term accuracy and precision would be difficult to achieve (KLIJUNAS et al. 2009).

2.3 *Ribes* eradication

Owing to their inextricably linked nature as alternate hosts of *C. ribicola*, *Ribes* have always been obvious targets for disease control. ZAMBINO (2010) describes *Ribes* biology, ecology, and role as a telial host of blister rust. Although MALOY (1997) has reviewed the broader history of blister rust control, we offer this synopsis on *Ribes* eradication to illustrate several key past and present aspects of silvicultural management in western North America.

British Columbia did not initiate a *Ribes* eradication programme because of its vast area and steep terrain (HUNT 2009). In the United States, more effort was placed on eradicating *Ribes* than any other control method (MALOY 1997). The three basic activities in this approach included: (1) reconnaissance to locate *Ribes*; (2) mechanical and chemical eradication (see ZAMBINO 2010: Fig. 1); and (3) monitoring to determine that all plants within local control areas were eliminated.

Although blister rust was not discovered in California until 1936, *Ribes* eradication had already begun as early as 1926 on an experimental basis in the central Sierra Nevada (BENEDICT and HARRIS 1931). Eradication of *Ribes* was directed by the Office of Blister Rust Control (OBRC) and during the Great Depression era carried out by the Civilian Conservation Corps (DETWILER 1933). Under the OBRC, activities were coordinated with other federal agencies including the Forest Service, National Park Service, Bureau of Land Management, and Bureau of Indian Affairs. The OBRC and public relief agencies were eventually discontinued, and federal land management agencies assumed direct responsibility for protecting white pine and eradicating *Ribes*. State and private lands were treated with matching funds from the states. California, for example, responded very aggressively and became one of the largest state contributors. At first, the objective of the control programme in Oregon and California was to eradicate *Ribes* wherever sugar pine grew, an area estimated at 1 million ha. When it became clear this goal was unattainable, the treatment area was reduced to 242 800 ha of the best sugar pine land (BENEDICT 1981).

Ribes eradication continued for >40 years in the United States, and millions of hectares were treated (MALOY 1997). *Ribes* eradication programmes in the western United States were terminated in the late 1960s because of increasing programme costs (labour) and the practical difficulty of eliminating common, native plant species across a large area (KETCHAM et al. 1968; MACGREGOR 1969). Control emphasis shifted to breeding for genetic resistance (BINGHAM 1983) and use of antibiotic fungicides (MOSS 1961). Although many *Ribes* bushes escaped destruction, many white pine stands benefited from a delay and reduction in blister rust intensification (MATTHEWS and HUTCHISON 1948; VAUX 1948). Although chemical treatment of troublesome vegetation is discouraged in North America for environmental reasons, telial host eradication is practiced in eastern Asia to protect forest plantations (KIM et al. 2010; ZHANG et al. 2010).

Most advice for raising white pines in nurseries focuses on three recommendations. The first is to eradicate all *Ribes* from the area immediately surrounding the nursery. Although

the usual recommended distance is 275 m, a buffer of 1.6 km is advised where highly susceptible European black currant (*R. nigrum* L.) bushes are present (BAXTER 1952). The second is to treat seedlings with a fungicide (usually with the active ingredient triadimefon) to protect against infection. Last is to grow the stock indoors to prevent blister rust from establishing prior to lifting the stock for replanting.

Several species of *Pedicularis* and *Castilleja* were recently determined to be additional telial hosts for *C. ribicola* in Idaho (McDONALD et al. 2006). Species of *Pedicularis* commonly serve as telial hosts for *Cronartium* rusts in Asia (KIM et al. 2010). In western North America, however, the epidemiological significance of these other telial hosts and their relevance to white pine silviculture are unknown. For example, were infections from these other telial host responsible for some apparent failures of *Ribes* eradication to control blister rust?

3 Regenerating stands

3.1 Harvesting and site preparation

Harvesting and site preparation provide an opportunity to reduce the regeneration of *Ribes* that could pose a hazard. BAXTER (1952) advocated winter logging to limit disturbance of duff and reduce *Ribes* colonization. He further suggested that tree removals be kept to a low volume to minimize canopy opening that could stimulate vegetative growth of *Ribes*. QUICK (1954) noted that vigorous growth of *R. roezlii* can occur for 25–30 years following harvest of a dense forest.

Several agencies are experimenting with controlled burns and innovative silvicultural cuttings that mimic natural fire for regenerating white pine stands (KEANE 2001b; SAMMAN et al. 2003). However, burning for site preparation carries both benefits and risks. Fire exposes mineral soil in which white pines regenerate (GRAHAM 1990; KINLOCH and SCHEUNER 1990; KLINKA et al. 2000). Fire creates open areas where Clark's nutcrackers (*Nucifraga columbiana*) cache the bird-dispersed seeds of limber pine (*P. flexilis*) and whitebark pine (LANNER and VANDER WALL 1980). Broadcast burning after clearcutting destroys *Ribes* seeds in the duff (BAXTER 1952). On the contrary, fire often burns at low intensity in some spots, sufficient to stimulate *Ribes* germination (MOSS and WELLNER 1953). For numerous western white pine plantations, site preparation with a bulldozer produced less *Ribes* regeneration than broadcast burning and resulted in less blister rust infection (SCHWANDT and FERGUSON 2003). An understanding of *Ribes* biology, site-specific knowledge of local situations, and monitoring are useful for minimizing the risk associated with a resurgence of *Ribes* (see ZAMBINO 2010).

3.2 Silviculture and genetic resistance

Western white pine and sugar pine threatened by *C. ribicola* are principally regenerated on intensively managed sites by planting resistant stock (KING et al. 2010). Where silviculture relies on naturally occurring seed sources for white pine regeneration, the prior selection and retention of genetically fit trees is important (BURNS et al. 2008; CONKLIN et al. 2009). The silvicultural issues discussed here are the use and performance of improved stock, associated management guidelines, and silvicultural practices for protecting genetic resources.

3.2.1 Western white pine

The Moscow, Idaho-based genetics programme has advanced to an operational stage for mass production of second generation (F₂) western white pine with improved blister rust

resistance (BINGHAM 1983; KING et al. 2010). With expectations that fewer of these trees would be infected and those which were would survive longer than natural regeneration, about 101 170 ha have been planted since 1976 in the Inland Northwest (northern Idaho and adjacent areas) (SCHWANDT and FERGUSON 2003).

SCHWANDT and FERGUSON (2003) assessed field performance after 9–20 years of improved western white pine stock from the Idaho programme and developed a set of management guidelines for use of this F₂ stock. Although <34% of improved stock were expected to be susceptible, the incidence for 66 surveyed plantations ranged from 0 to 96% (severity and mortality were correlated to incidence). Only 52% of plantations performed up to or better than the expectation; even so, the average incidence for F₂ stock was about half that of adjacent natural regeneration.

Based on field trials for the Idaho F₂ stock, SCHWANDT and FERGUSON (2003) observed for plantations in northern Idaho that:

- F₂ white pine can be expected to perform better than natural white pines in terms of fewer infections, lower mortality, and greater longevity of infected trees;
- incidence in F₂ plantations can vary greatly from the expected maximum of 34%, but a longer monitoring period is required to determine if the present high incidence in trees 10–20 years old would eventually result in a delayed, high-mortality rate;
- plantations should not be planted with only F₂ white pine but be composed of mixed species;
- pruning has doubled survival in young natural stands and might do as well in F₂ plantations;
- periodic monitoring is necessary to determine if additional treatment such as pruning would be beneficial and to better recognize site hazard associated with the local climate and *Ribes* populations;
- planting a high density of F₂ stock could increase white pine representation on some sites;
- but MULLER'S (2002) hazard model needs additional testing to justify its broad application and determine which sites would benefit from planting higher densities of F₂ stock.

A field trial of Idaho F₂ material at two sites in coastal British Columbia showed that 60 and 95% of seedlings were infected 29 years after planting, rates higher than generally occur in the Inland Northwest or interior of British Columbia (HUNT 2004a). The discrepancy in performance led HUNT (2004b) to speculate there might be a gene-by-environment interaction. A milder climate and longer growing season in coastal British Columbia than inland and interior regions might favour pathogen infection and disease expression (HUNT 2005). Consequently, Idaho F₂ stock is considered useful for reforestation in interior British Columbia but not in coastal districts. Although HUNT and MEAGHER (1989) observed that eastern white pine seedlings were less frequently infected in coastal British Columbia plantations than local western white pine, eastern white pine were undesirable because of their excessive branching and forking.

3.2.2 Sugar pine

A tree selection and screening programme for sugar pine associated with the Institute of Forest Genetics (USDA Forest Service, Placerville, CA, USA) discovered the first R gene found in a forest tree species (KINLOCH et al. 1970). This R gene, designated as *Cr1*, confers immunity through a hypersensitive reaction (HR) in needle tissues when challenged by *C. ribicola* (see KING et al. 2010). Owing to its major effect and simple inheritance, this HR response has been called major gene resistance (MGR). Resistance is a dominant trait but is defeated by a virulent race. Similar R genes have been reported for western white pine, *Cr2*

(KINLOCH and DUPPER 1999) and for southwestern white pine, *Cr3* (KINLOCH and DUPPER 2002) and hypothesized for limber pine (VOGLER et al. 2006). Current work is attempting to include both partial resistance (by which trees survive longer even if infected by a virulent race) and R-gene resistance (KINLOCH et al. 2008).

The goal of the sugar pine programme in California is to preserve the genetic integrity of sugar pine populations at risk from blister rust by developing durable resistance based on multiple mechanisms (SAMMAN and KITZMILLER 1996). The approach is to: (1) develop an action plan for each forest; (2) preserve apparently resistant trees; and (3) apply appropriate silviculture to stands with sugar pine to protect the genetic base. Federal, state, and private land managers use a cooperative approach that includes finding rust-resistant candidate trees, collecting cones, screening for resistance, collecting and storing resistant seed, planting resistant seedlings, establishing seed production orchards, and protecting resistant trees from insect, disease and animal pests (SAMMAN and KITZMILLER 1996; VIOLETT et al. 1996).

Although resistant seed has priority for use, its supply for some sites is limited; so, planting includes a mixture of resistant seed (from selected parents) and untested seed (from local forest collections). Resistant sugar pine are planted at a rate of ~100 trees per ha in a mixture with other conifers to obtain approximately 10% sugar pine in the mature stand.

3.2.3 R-gene deployment in Canada

The Dorena Genetic Resource Center (USDA Forest Service, Dorena, OR, USA) has made seed and pollen with *Cr2* available for reforestation of western white pine in Canada. Although *Cr2* is not known to occur naturally in British Columbia, it can be incorporated into local seed sources to increase resistance while retaining locally adapted traits. Ideally, trees possessing both R-gene resistance and partial resistance will become available (HUNT 2003b).

3.2.4 Protecting genetic resources

The effort to find candidate resistant trees, collect cones, and test seeds is a significant investment of time and money. When a candidate white pine is proved to be resistant, it becomes extremely valuable. This is particularly true for sugar pine where it becomes an *in situ* seed source. Protecting an investment often requires additional silvicultural treatments. Trees in dense aggregations or subject to drought are vulnerable to bark beetle attack, principally by mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Therefore, many managers thin or clear vegetation adjacent to resistant-proven white pine trees. During droughts, individual trees have been watered with drip irrigation systems and sprayed with carbaryl to prevent bark beetle attack (VIOLETT et al. 1996). Thinning reduces cone loss to squirrels by increasing the distance between tree crowns. Often a metal 'squirrel band' is installed on the lower stem of a resistant tree to prevent squirrels from reaching cones by climbing up the bole. Another practice is to place mesh bags on immature cones to protect them from *Conophthorus* cone beetles and birds.

3.3 Seedling protectors

In many areas of western North America, browsing by deer (*Odocoileus*) and elk (*Cervus*) severely damages white pine seedlings. Various devices are available to protect young trees from browse damage until leaders are less vulnerable (BOOTH and HENIGMAN 1996). Solid protectors provide several additional benefits. They act as a physical barrier to *C. ribicola* basidiospores (preventing infections that are usually lethal in the susceptible lower crown), and they create a mini-greenhouse effect (promoting rapid seedling growth). The

effectiveness of these protectors for reducing blister rust infection in western white pine was demonstrated in one small trial (HUNT 2002a) and is currently being testing in a comprehensive study (R. Diprose, personal communication).

4 Tending established stands

4.1 Thinning

Although thinning to rid a white pine stand of infected trees and thereby reduce aeciospore production has been advocated to control *C. ribicola*, the effects of opening a young stand on basidiospore dispersal, self-pruning, and *Ribes* growth should be considered. MIELKE (1943) and KIMMEY and WAGENER (1961) proposed that dense foliage screened basidiospores from effective dispersal and contributed to a rapid decline in infection with distance from an inoculum source. HUNT (1998) observed that blister rust infections low in the crown and close to the bole (lethal cankers) were more frequent in open stands of young western white pine. HUNGERFORD et al. (1982) determined that early thinning in Idaho not only reduced natural, early pruning of young western white pine but also encouraged *Ribes* growth.

Thinning recommendations consider the operational choices of stand age, tree selection, and desired stocking (BAXTER 1952; TAINTER and BAKER 1996). A delay in thinning until a western white pine stand is 25–30 years old provides benefits of screening, early self-pruning, and shading out *Ribes*. Initial effects of blister rust infestation are evident by that age and allow for selection with knowledge of which trees are infected and which would never produce a crop tree.

For mixed species stands with western white pine, FINS et al. (2002) recommended: (1) removing other species first where white pine densities are low; (2) thinning only around potential crop trees and shade-intolerant species and leaving the remainder unthinned ('daylighting'); and (3) retaining a high density where white pine are abundant. For British Columbia, HUNT (1998) suggested retaining at least 700 stems per ha. Residual stand density is often used as a target for assessing a thinning contractor's performance. Where white pine trees form a minor component of a stand, their retention could be encouraged by declaring them as 'ghost trees' exempt from thinning and excluded from a final tree tally. In the Southwest, CONKLIN et al. (2009) advocate retaining more white pine trees to compensate for later blister rust mortality and to increase the likelihood of maintaining any resistant trees on the site. For maximizing white pine survival, SAMMAN et al. (2003), FINS et al. (2002), and SCHWANDT et al. (1994) suggested that thinning be performed in conjunction with pruning. Operationally, pruning should precede thinning, so that cankered but prunable trees would not be cut while unprunable trees (e.g., with a large basal canker) are retained. Accumulations of thinning slash might also conceal potentially infected lower branches from pruners (SCHNEPF and SCHWANDT 2006).

4.2 Pruning and excising cankers

Pruning to reduce damage from *C. ribicola* has been recommended since 1929 in Canada (MCCALLUM 1929) and earlier in the United States (MARTIN et al. 1921). It is still the principal silvicultural method for ornamental plantings (PSCHIEDT and OCAMB 2008) as well as forest stands (BRITISH COLUMBIA MINISTRY OF FORESTS 1995, 1996). Pruning is used for white pine blister rusts in China and South Korea (ZHANG et al. 2010; KIM et al. 2010). It is also used for: (1) *C. comandrae* Peck (JOHNSON 1986) on lodgepole pine (*Pinus contorta* Dougl. ex Loud.); (2) *C. quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* (fusiform rust) on southern pines (PHELPS and CZABATOR 1978) in North America; and (3) *C. flaccidum* (KAITERA 2002) on Scots pine (*P. sylvestris* L.) in Europe.

4.2.1 Why prune?

The objective of sanitation pruning is to improve the survival of trees already infected; the objective of preventative pruning is to reduce future blister rust infection by removing vulnerable branches and altering the environment. The benefits of removing infected branches, branches likely to develop lethal cankers, and knot-forming branches are easy to recognize. The effectiveness of pruning on altering the microclimate is not so obvious. Infection is favoured by cool, humid air (TAINTER and BAKER 1996). Removing lower branches ('lifting the crown') could increase light penetration and air circulation near the ground, but whether increased ultra-violet radiation, heat, or aridity significantly reduces infection rate would be difficult to demonstrate. Pruning studies have produced variable and non-comparable results on the subsequent number and distribution of infected branches owing to differences in stand age, location, species composition, and treatment (e.g., pruning only, thinning only, pruning followed by thinning).

The practical indicator that pruning is effective has been a reduction in mortality from blister rust. HUNT (1982) found that approximately 50% of blister rust cankers on the stems of western white pine 12–30 years old and representative for British Columbia originated below 1.25 m and 75% were below 2.5 m. Prompt removal of lower branches could therefore prevent stem cankers likely to be lethal. Similar observations and conclusions have been made for eastern white pine (WEBER 1964; LEHRER 1982; OSTRY et al. 2010). For western white pine and sugar pine, the efficacy of pruning has been repeatedly demonstrated (HAYES and STEIN 1957; BYLER and PARMETER 1979; HUNGERFORD et al. 1982; BEALE 1988; HAGLE and GRASHAM 1988; RUSSELL 1988; HAGLE et al. 1989; HUNT 1991, 1998; SCHNEPF 2002; BISHAW et al. 2003). Because pruning is labour-intensive, it has usually been used in commercial stands but pruning can also enhance survival of any high-value white pine for aesthetic or biodiversity values.

4.2.2 Where and when to prune?

Whether pruning would reduce infection and mortality in a particular stand depends on site hazard and site productivity. On a high-hazard site, incidence and severity are expected to be large, infection to occur frequently, and canker distribution to extend high into the crown. HUNT (1983) observed more cankers higher in the crowns of western white pines on sites with steep slopes than flat sites. An interaction of site productivity and regeneration history affects the composition, density, and early height growth of white pine trees that determines if and when pruning would be effective.

In many early studies (HUNGERFORD et al. 1982; BEALE 1988; HUNT 1991), western white pine trees approximately 10–20 years old were pruned in stands where blister rust infection and early mortality had already peaked. The special character of these stands led to a conclusion that pruning and thinning should be delayed a sufficient time to allow expression of blister rust selection and capture the benefits of a release response by survivors. A recent review by SCHNEPF and SCHWANDT (2006) of additional studies concluded that blister rust pruning would be most effective when open groupings of western white pine trees were younger than 25 years old and that tall, dense groupings should be left to self-prune.

SCHNEPF and SCHWANDT (2006) suggested a manager in the Inland Northwest ask three questions before pruning a stand. The first question is whether the trees are younger than 25 years? This ensures trees that would most benefit from pruning are present and that treatment would be applied when live branches occupy the lowest portion of the bole. The second question is how many trees can be saved by pruning? Where many trees are infected and lethal stem cankers are common, pruning would ultimately save few trees. Where incidence is low, pruning could be delayed until acceptable stocking is threatened by blister

rust. The timing and frequency of pruning depends on expected costs and returns. For small-operation landowners with intensively managed woodlots, frequent assessment and pruning could be feasible. For commercial forest companies with extensive plantations, a single entry dictated by labour costs and the risk of blister rust to stocking goals would be preferred. The final question is does the site have a high or low potential for new blister rust infections (site hazard)? On climatically favourable sites where *Ribes* provide abundant inoculum, no amount of pruning would be sufficient to prevent severe stocking losses.

Western white pine sites in coastal British Columbia and Washington state tend to be more productive than those in the Inland Northwest; so, early and frequent pruning has been recommended (RUSSELL 1988; HUNT 1991; BRITISH COLUMBIA MINISTRY OF FORESTS 1996; ZEGLEN et al. 2009). A typical regime is to begin pruning trees 3–5 years after planting and to follow up a few years later with one or more prunings. This procedure aimed at removing the most vulnerable, lower portion of the canopy as soon as possible is similar to that long advocated to control blister rust on eastern white pine (WEBER 1964).

4.2.3 How much to prune?

In many pruning studies, branch cankers are divided into three categories depending on their proximity to the bole (trunk) and therefore their likely fate as non-lethal cankers, lethal-unprunable cankers, and lethal-prunable cankers (HAYES and STEIN 1957; HUNT 1982). Non-lethal cankers are those infections far enough out a branch that mycelial growth into the bole is unlikely even if the branch is not removed by sanitation pruning. Lethal-unprunable cankers are those infections with the canker margin close enough to the bole such that fungal mycelia are likely to have already advanced into bole (EHRlich and OPIE 1940). Lethal-prunable cankers (also called threatening cankers) are those infections restricted to a branch but expected capable of reaching the bole if not removed. Sanitation pruning of prunable branches benefits tree survival (DENITTO 1996). As pruning is typically considered for trees <25 years old with infections within the lower few meters of the crown, cankers that girdle the bole are usually lethal because so much of the crown is killed. For older trees with infections in the top of long or multi-stemmed crown (such as sugar pine or whitebark pine), a girdling stem canker can be considered as 'lethal' in the sense it causes topkill, although the tree survives.

Pruning requires a balance between removing branches to eliminate cankers and protect against future infection and retaining sufficient live crown to insure tree survival and growth. The distribution of cankers and crown size vary with numerous factors, including species, age, site productivity, stand density, and blister rust hazard. Pruning prescriptions usually specify treatment in terms of an average size of trees eligible for pruning, a maximum percent of live crown removed at a single treatment, and a final target pruning height (Table 1). Usually, pruning western white pine is initiated after average tree height exceeds 1–3 m. About half of the crown is always retained; and pruning for blister rust control is repeated until the live crown base is higher than 2.4–3 m. For very productive sites in Washington state, RUSSELL (1988) showed that western white pine as short as 0.2–1.5 m could be pruned without growth loss if at least two whorls below the leader are left intact. Treatments this aggressive, however, are rarely applied in the West but are recommended for eastern white pine (WEBER 1964; NICHOLLS and ANDERSON 1977). The distribution of blister rust cankers on western white pine resembles that of eastern white pine and pruning guidelines is similar. In contrast, sugar pine is infected sufficiently often to a crown height of 5.5 m that its target pruning height is adjusted upward.

Special care ensures that branches buried in the duff at the base of the tree are not missed. For sugar pine, HAYES and STEIN (1957) found that it took the same time to remove all branches to a target height as it did to search for, and remove, only infected branches.

4.2.4 Associated hazards

Several hazards are associated with pruning. Pruning creates a fire hazard if large quantities of slash are left on site. As pruning is often conducted in autumn, freshly cut boughs could be sold for economic return (SCHNEFF and SCHWANDT 2006; ZEGLEN et al. 2009). Red turpentine beetles (*Dendroctonus valens* LeConte) are attracted to slash and fresh pruning cuts (HAGLE and GRASHAM 1988). While these bark beetles rarely become numerous, they can kill a small number of trees, particularly on drought-stressed sites. Although young white pines tend to have relatively open canopies, pruning combined with thinning during hot, dry weather could subject some trees to sunscald (BRITISH COLUMBIA MINISTRY OF FORESTS 1995). While this affliction is rarely fatal, sunscald would produce a long wound attractive to wood borers and decay fungi.

4.2.5 Excising cankers

In conjunction with pruning, excising or scribing stem cankers or large branch cankers has been used to save trees with potentially lethal cankers (BAUMAN 1970). The technique, first described for ornamental white pines by MARTIN et al. (1921), involves removing the bark in a band at least 5 cm from the side edges of the canker and 10 cm from the upper and lower edges. So that fungal mycelia do not bridge the gap, all the inner bark is removed down to the sapwood. Excision is usually attempted only if <50% of the stem circumference would be removed. HAGLE and GRASHAM (1988) observed an 81% success rate after 15 months with excising cankers on 18-year-old western white pines in Idaho. Because it is labour-intensive, scribing is usually reserved for ornamental or other high-value trees (SCHNEFF and SCHWANDT 2006; ZEGLEN et al. 2009).

4.2.6 Economics and other values

While the economics of pruning trees for product value has been studied extensively (HORTON 1966), there has been little examination of the costs and benefits of pruning specifically to control white pine blister rust. Thinning, pruning, and excising cankers are silvicultural activities that would incur costs for planning, implementing, and monitoring but could provide benefits from increased growth, survival, and value of white pine. Is the investment worth the risk? HAGLE and GRASHAM (1988) determined that a pruning and scribing treatment could be economically feasible if afterwards white pine trees composed a

Table 1. White pine pruning thresholds and tolerances white pine blister rust in North America.

	Start pruning (average tree height, m)	Maximum live crown removal (%)	Target pruning height (m)	Lethal canker distance ¹ (cm)	Non-lethal canker distance ² (cm)
Western white pine					
BC coast ³	1.0–2.5	65	3.0	–	60
BC interior ³	1.0–2.5	50	3.0	–	60
Inland Empire ⁴	1.5–3.0	50	2.4	10	–
Sugar pine ⁵	–	50	5.5	10	60
Eastern white pine ⁶	0.6	50	2.8	10	–

¹Branch cankers closer than given distance to bole are likely to have already infected bole.
²Branch cankers further than given distance to bole are unlikely to ever infect the bole.
³BRITISH COLUMBIA (BC) MINISTRY OF FORESTS (1996).⁴SCHNEFF and SCHWANDT (2006).⁵BYLER and PARMETER (1979), HAYES and STEIN (1957).⁶FUNK (1961), WEBER (1964), NICHOLLS and ANDERSON (1977).

substantial portion of a stand and the non-pine species were physically smaller at the time of treatment and less valuable than the white pine.

In addition to value for wood products, white pine trees provide numerous ecological benefits (TOMBACK and ACHUFF 2010). Thinning, pruning, and excising cankers are among the few silvicultural practices that might increase the survival and longevity of white pine threatened by blister rust. As in an economic assessment, the factors to consider are related to blister rust hazard and risk; but the value is to protect a tree for other social, ecological, or biological reasons.

4.3 Biological control

Several organisms compete for space and resources with *C. ribicola* (WILLIAMS 1972). Conifer needles have naturally occurring endophytic fungi, some of which appear to control blister rust (BÉRUBÉ et al. 1998; GANLEY et al. 2008). However, very few of these potential biocontrol fungi have been investigated in sufficient detail to provide a practical management tool.

The purple mould, *Tuberculina maxima* Rostr., often occurs on cankers infected by a *Cronartium* rust. As early as 1901, Carl von Tubeuf was studying *T. maxima*; he later applied the term 'biological control' for the first time to describe its effect on *C. ribicola* (MALOY and LANG 2003). As *T. maxima* colonizes rust cankers producing pycnia and aecia (MIELKE 1933), it appeared to have a good potential for controlling blister rust (HUBERT 1935). Unfortunately, application met with little success (QUICK and LAMOUREAUX 1967), because *T. maxima* mainly colonizes older rust cankers (KIMMEY 1969) and often dies before overrunning the *C. ribicola* infection (WICKER and WOO 1973). WICKER (1981) finally clarified that *T. maxima* is not a hyperparasite infecting *Cronartium* but only degrades rust-infected, host-cortical tissues; although the mould limits rust sporulation, it does not eliminate the infection.

4.4 Chemical control

Owing to the perceived impracticality and expense of pruning branches and scribing cankers, an extensive search was instituted in the early 1950s for chemical controls of *C. ribicola* (MOSS 1961). Because phytoactin and cycloheximide appeared to be effective on other tree pathogens, these 'antibiotics' were further tested as fungicides for systemic control of blister rust (MOSS 1961). Although early results suggested that phytoactin was not very effective, a formulation of cycloheximide historically marketed as Actidione BR® was considered quite promising (MOSS et al. 1960). Application consisted of dissolving the fungicide in a fuel-oil carrier and either sprayed from the ground on to the lower bole or from the air into the crown. Early field trials were conducted in 1959 on western white pine in Idaho by ground spraying and shortly thereafter in British Columbia and the Rocky Mountains by aerial application (VICHE et al. 1962; GLEW and MACLOED 1963). By the late 1960s, additional studies were conducted for numerous host species such as western white pine (LEAPHART and WICKER 1968), eastern white pine (PHELPS and WEBER 1968), and whitebark pine (BROWN 1969). When these latter studies demonstrated that neither phytoactin nor cycloheximide was effective on blister rust, further research and application were discontinued.

Although many fungicides tested in the 1960s and 1970s were ineffective in killing blister rust (HUNT 2003a), several fungicides could protect trees from infection. In the southeastern United States, triadimefon is applied to seeds and seedlings of slash pine (*P. elliottii* Engelm. var. *elliottii*) and loblolly pine (*P. taeda* L.) to protect against fusiform rust (POWERS 1984; KELLEY and WILLIAMS 1985). Greenhouse tests using triadimefon and benodanil indicated sugar pine seedlings were systemically protected for at least several weeks from infection by

C. ribicola (JOHNSON et al. 1992). A similar test using just triadimefon was successful for eastern white pine (BÉRUBÉ 1996). Although planting western white pine with triadimefon-impregnated pellets provided good disease control, seedling growth was stunted (HUNT and WEBB 1995). Eastern white pine planted with triadimefon-impregnated pellets and fertilizer had lower infection and mortality rates for at least seven growing seasons; and at one study site, where weeds were also controlled with herbicides, the trees also had better growth (PITT et al. 2006). Triadimefon (as Bayleton® Bayer Cropsciences AG, Monheim am Rhein, Germany) is registered in the United States for use on Christmas trees (PSCHIEDT and OCAMB 2008). Chemical treatment is especially useful for protecting nursery trees from infection in areas where *Ribes* eradication is not feasible.

5 Conclusion

Over the last century, foresters and researchers have battled *C. ribicola* on white pines across North America with mixed success. *Ribes* eradication might have reduced blister rust severity in the first wave, but *Ribes* are resilient. Except for limited cases of protecting high-value white pine, eradication is no longer practical for economic and ecological reasons. Site hazard for blister rust can be assessed; *Ribes* regeneration and growth can be minimized at a local scale by site preparation and canopy management. Thinning and pruning can reduce losses to blister rust but are expensive. Cultural treatments are practical where costs are offset by economic increases in yield and quality or by the ecological benefits of maintaining white pine on a site. We have no proved agents for classical biological control, although possibilities remain for innovative methods of managing biotic associates. Chemicals that kill the pathogen without collateral damage are unknown, but there is a limited role for a few protective fungicides and herbicides.

Traditional tree breeding has also had mixed success in producing seedlings that are either resistant to blister rust or survive with disease. Early expectations for the Idaho F₂ western white pine proved overly optimistic, but these F₂ seedlings still outperformed naturally regenerated trees. Several species of white pine have a single, dominant gene that confers immunity to *C. ribicola*, but R genes may be defeated by virulent races of blister rust fungi.

Managing white pine requires both genetics and silviculture—genetics to increase a population's inheritable capacities for resistance and survival and silviculture to protect genetic resources, increase regeneration, reduce blister rust damage, and increase stand volume and wood product quality. Genetics and silviculture applied in a cooperative, learning framework provide an adaptive management approach for preventing loss of white pine populations and returning them to their previous biological, ecological, and commercial roles in western North American forests.

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