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SITE AND STAND CHARACTERISTICS RELATED TO WHITE PINE BLISTER RUST IN HIGH-ELEVATION FORESTS OF SOUTHERN IDAHO AND WESTERN WYOMING¹

Jonathan P. Smith² and James T. Hoffman³

ABSTRACT.—Successful infection of white pine species by white pine blister rust (WPBR) is contingent upon environmental conditions that are favorable to the spread and development of *Cronartium ribicola*. Site and stand factors related to this process have been studied elsewhere within the distribution of the disease, but few studies have concentrated on the high-elevation white pine forests of southern Idaho and western Wyoming. We found that mean summer precipitation, average tree diameter, and elevation were the most important variables in 3 logistic regression models of WPBR presence and intensity. The models were tested on a randomly chosen portion of our data set. The model with 9 variables correctly predicted categories of low-, moderate-, and high-disease incidence in 79% of cases. The 2 models with fewer variables had lower predictive efficiencies but were more parsimonious and generally easy to measure. The ability to use easily measured or remotely sensed site and stand characteristics to predict WPBR spread or intensification could be an important asset to land managers who need to decide where to focus disease mitigation efforts and predict disease effects on water quality, wildlife habitat, recreation potential, and other land-management activities.

Key words: white pine, whitebark pine, limber pine, white pine blister rust, *Cronartium ribicola*, tree diseases, Rocky Mountain forests, subalpine forests.

White pine blister rust disease (WPBR), caused by the introduced fungus *Cronartium ribicola*, is the most widespread and serious disease of *Pinus albicaulis* (whitebark pine; Arno and Hoff 1989) and *P. flexilis* (limber pine) in the Rocky Mountains (Smith and Hoffman 2000). The disease is also a potential threat to most, if not all, other white pine species (genus *Pinus*, subgenus *Strobus*, section *Strobus*, subsections *Cembrae* and *Strobi*, and section *Parrya*, subsection *Balfourianae*; Hoff et al. 1980). The rust causes branch and stem cankers that, in most cases, girdle and kill the host tree.

Cronartium ribicola has a complex life cycle that is characterized by 5 spore-producing stages that alternate infection between white pine species and plants of the genus *Ribes* (currants and gooseberries). Aeciospores are small, light spores that are produced on pine cankers and can travel long distances to infect the leaves of *Ribes*. Urediniospores emerge on *Ribes* leaves and spread to other leaves on the same plant, or other nearby *Ribes* plants. Teliospores, produced on *Ribes*, germinate and form the basidium, which releases basidio-

spores to infect white pine needles. Fungal hyphae spread into woody tissue causing cankers, where the 5th type of spore-bearing structure, the pycnium, is produced. Upon completion of the pycnial stage, which probably involves mating, aecia are produced, completing the life cycle.

Like other pine rusts, transmission of spores and host infection depends on a favorable temperature and moisture environment, an abundance of spores (inoculum), and availability of susceptible hosts (Mielke 1943, Charlton 1963). These conditions may be affected by physical factors such as slope, aspect, elevation, and precipitation, as well as biological factors such as structure of the forest canopy and proximity of *Ribes* spp.

Site and stand factors associated with rust incidence have been identified by studying the distribution of WPBR and endemic pine rusts. Van Arsdel (1972) found that the size of forest canopy openings and certain topographic features were related to WPBR incidence in *Pinus strobus* (eastern white pine). In British Columbia, Hunt (1983) reported more WPBR

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cankers in *P. monticola* (over 2.5 m high in the tree) as slope increased. Jacobi et al. (1993) found *Cronartium comandrae* (comandra blister rust) incidence in *Pinus contorta* subsp. *latifolia* (lodgepole pine) positively correlated with tree diameter, and negatively correlated with stand density and distance to the rust's telial host. Beard et al. (1983) found a greater incidence of *C. coleosporioides* (stalactiform blister rust) in central Idaho *Pinus contorta* forests at middle to upper elevations, and in *Abies lasiocarpa*/*Xerophyllum tenax* and *Abies lasiocarpa*/*Vaccinium scoparium* habitat types. *Endocronartium* (= *Peridermium*) *harknessii* (western gall rust) stem infections were negatively correlated with stand age in British Columbia *Pinus contorta* forests (van der Kamp 1988). Van Arsdell (1965) constructed a formula based on slope and canopy openings and predicted WPBR presence in southwestern Wisconsin with 89% accuracy. Charlton (1963) used aspect, elevation, slope, topographic position, and vegetation structure, along with climatic factors, to assess WPBR infection hazard in the eastern U.S. A comprehensive site-specific WPBR hazard model based on site, stand, alternate host, and physiological factors was developed by McDonald et al. (1981) for *P. monticola* in northern Idaho.

Very little of this type of work has been conducted in the southern portion of *C. ribicola*'s range in the Rocky Mountains because, historically, disease surveys revealed only trace levels of infection (Brown 1967, Brown and Graham 1969). However, WPBR has recently intensified and spread to new locations in the southern portions of the Northern Rocky Mountain and Middle Rocky Mountain provinces (Kendall et al. 1996, Smith and Hoffman 2000). As an initial step in modeling WPBR spread and intensification in this region, we used USDA Forest Service disease survey data (Smith and Hoffman 1998) to look for relationships between WPBR incidence and several site and stand characteristics.

STUDY AREA

Pinus albicaulis and *P. flexilis* populations in the U.S. extend southward along the Rocky Mountains from the Canadian border to southeastern Idaho and southwestern Wyoming. *Pinus flexilis* extends even further south, throughout the mountains of Utah. There are

also several disjunct *P. flexilis* and *P. albicaulis* populations in isolated mountain ranges of eastern Oregon and northern Nevada, and both species occur in the Sierra Nevada (Critchfield and Little 1966). Our study area encompasses those Rocky Mountain white pine populations that lie within southern Idaho and western Wyoming (Fig. 1). Within this region *P. albicaulis* and *P. flexilis* populations extend upward from the lower subalpine zone to the upper (cold) tree line. *Pinus flexilis* also has the unique ability to grow at lower (dry) tree line (Arno and Hammerly 1984).

FIELD METHODS

In 1995 we installed 10 rectangular plots according to the methods specified by the Whitebark Pine Monitoring Network (Kendall 1995). In 1996 we used randomly located strip transects rather than rectangular plots to delineate trees. We switched to transects because white pine species in our study area tend to grow as dispersed woodlands or as infrequent seral components in subalpine forests. Obtaining 50 white pines in a rectangular plot of a reasonable size was often not possible. For the 68 sites sampled during 1996, we established a 4.6-m (15-ft)-wide strip transect, along the contour of the slope, from a random starting point. We traversed this transect until 50 white pines had been inspected or until we encountered a change in the character of the site or stand that did not match our sampling criteria, such as a different canopy structure, a sufficiently different aspect (>10° difference), slope (>5% difference), habitat type or phase, or a topographic change. Rather than cross this environmental gradient, we changed the direction of the transect by 180°, displaced it uphill or downhill 4.6 m (15 ft), and continued to sample until 50 trees had been inspected.

For each tree we recorded the presence of WPBR cankers and DBH (diameter at breast height, 1.37 m above the ground), in 5.1-cm (2-in) size classes. At the midpoint of each transect, we measured or calculated habitat type (Steele et al. 1981, 1983), presence/absence of *Ribes* sp., basal area, trees per hectare, canopy closure, elevation, aspect, slope angle, and topographic position (Table 1).

An additional variable, estimated mean summer precipitation, was generated from climate maps (Martner 1986, Molnau and Newton

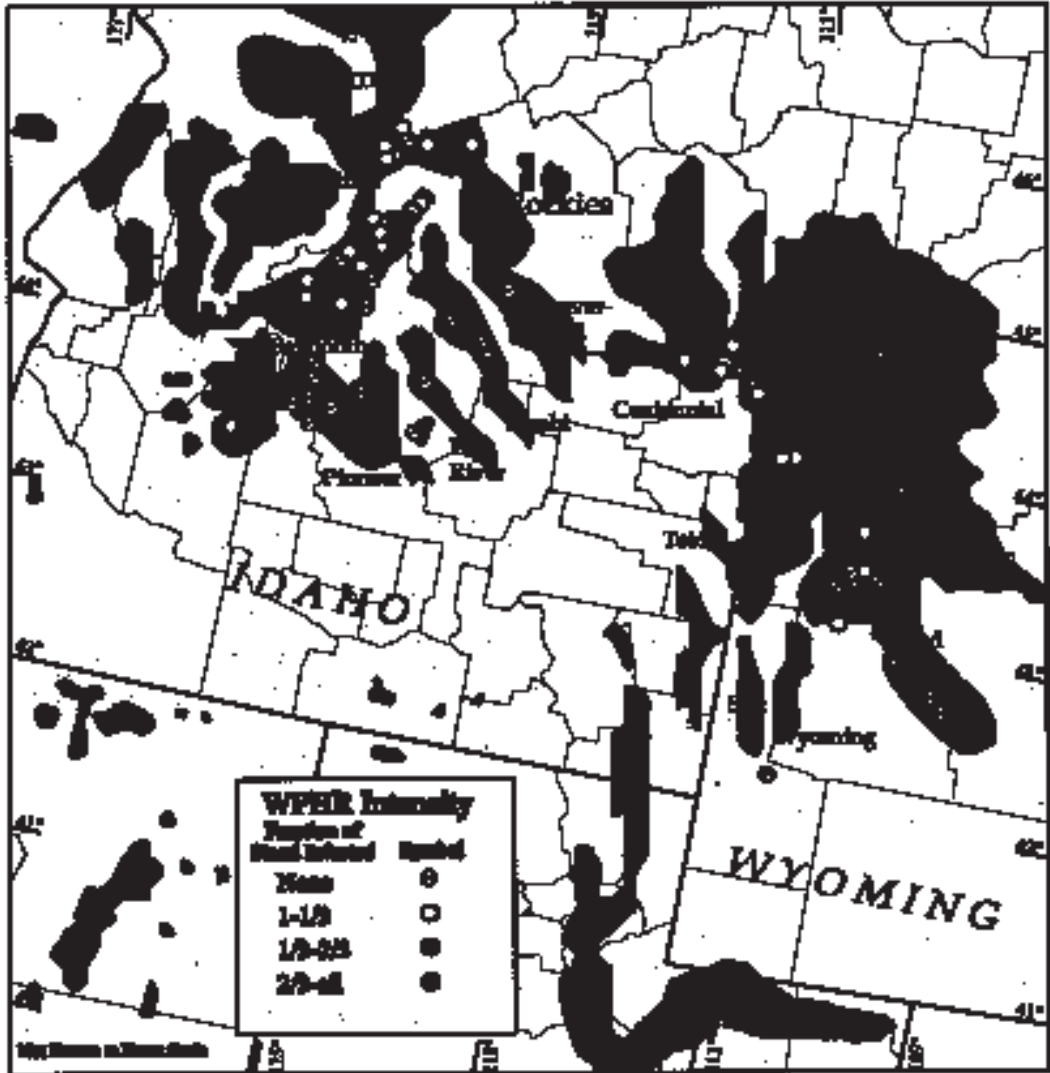


Fig. 1. Northern and middle Rocky Mountain ranges, sample locations, and white pine blister rust intensity for 78 sample sites inspected in 1995-1996. Distribution of white pine species (shaded areas) derived from Little (1971).

1994). To estimate mean summer precipitation, we multiplied regionalized estimates of the summer (June, July, and August) proportion of total precipitation by the mean annual precipitation values taken from these maps. We interpolated precipitation values between isohyetal contours for each of our sample sites.

STATISTICAL METHODS

Because sampling location criteria and data collection procedures were identical for plots and transects, the data were combined for our

analysis. We grouped the categorical independent variables, habitat type, canopy cover, and topography to reduce the number of categories for model calculation. For example, we identified 20 habitat type classes in the field but combined these into 4 categories based on a multidimensional scaling procedure that groups habitat series based on moisture requirements of understory plants (McDonald unpublished data). We used dummy coding for the categorical variables. Presence or absence of *Ribes* spp. was entered as a binary variable (i.e., a value of 0 for absent, 1 for present).

TABLE 1. Variables used in the stepwise logistic regression procedure and parameter estimates for the 3 models using the recombined (full) data set.

Variable (description)	Standardized parameter estimate (Wald χ^2)		
	Model 1	Model 2	Model 3
Elevation (meters, from topo map)	-0.613 (313)	-0.606 (321)	-0.546 (308)
Average DBH (diameter at breast height in 2-cm classes)	0.458 (212)	0.454 (210)	0.517 (301)
Mean summer precipitation (interpolated from maps)	0.278 (109)	0.304 (145)	0.250 (111)
<i>Ribes</i> (present/absent in stand)	0.237 (62)	0.239 (69)	
Stand density (trees · ha ⁻¹ , all species)	-0.258 (61)	-0.222 (55)	
Topographic position 3 (upper slopes)	0.215 (56)	0.212 (55)	
Habitat type 1 (wet subalpine fir group)	0.123 (28)		
Slope (percent)	-0.109 (12)	-0.118 (15)	
Habitat type 4 (whitebark pine series)	0.007 (7)		
Basal area (m ² · ha ⁻¹ , all species, white pines only)			
Aspect (cosine of aspect in degrees)			
Latitude (UTM-northing)			
Canopy (open, broken, closed)			
Topography (valley/lower, mid, upper, ridge)			
Habitat type (wet subalpine fir, cool/moist subalpine fir, cold/dry subalpine fir, whitebark series, Douglas-fir)			

Elevation, slope, latitude (UTM northing), average tree size, and mean summer precipitation were entered as continuous variables (i.e., their actual measured values). The aspect measurement, which is azimuthal (circular data), was linearized by taking the cosine of the aspect in radians.

Logistic Regression Analysis

Percent of trees infected in a sample stand was the dependent variable, which was treated statistically as the number of successful events (infected trees) per number of trials (trees sampled) at each sample site. We performed a stepwise logistic regression procedure with the model development data set using the PROC LOGISTIC STEPWISE option in SAS (SAS Institute Inc. 1996). This procedure identifies predictive variables when the number of potential explanatory variables is large relative to the number of samples (Hosmer and Lemeshow 1989). We constructed 3 models of WPBR incidence with combinations of the variables selected by the stepwise procedure.

To determine if models were statistically significant, we compared 4 criteria to assess how well the models fit and to compare how well each model predicted WPBR incidence. First, we calculated r^2_L , which is a measure of the reduction in the log-likelihood as a result of including the independent variables (Menard 1995). We tested the null hypothesis that the

predictor variables contribute no more than chance to the explanation of the dependent variable with the G_m statistic (the model chi-square statistic). The Bayesian information criterion (BIC) was calculated as a selection device because it emphasizes parsimony by penalizing models with a large number of parameters (Ramsey and Schafer 1997). To measure the predictive efficiency of each model, we arbitrarily assigned broad classes of WPBR incidence, low (<25% incidence), medium (26–50%), and high (>50%), to the observed and predicted values and then calculated how frequently each model correctly predicted the observed category, was 1 category off, or was off by 2 categories.

Model Testing

We used a split-sample validation technique to develop and test the logistic regression models. Each record was assigned a random number, sorted by this number, and then split into a model-development data set (2/3 of the data), which was used to develop the models. The remaining 1/3 of the data ($n = 23$) was treated as an independent data set to test the models' statistical significance, fit, and predictive efficiency, and to assess the importance of the independent variables. We estimated the predicted proportion of trees infected in each sample with the predicted probability of infection (presence or absence of WPBR) for each tree in that sample.

TABLE 2. Fit statistics and prediction efficiency for 3 logistic regression models of WPBR incidence using the model-developing data set (A) and the model-validation data set (B).

A								Prediction of incidence category				
Model	χ^2 's	G_M^a	P^b	R^{2c}	$R^2_L^d$	BIC ^e	n^f	Correct	Under 1	Over 1	Under 2	Over 2
1	9	502	0.001	0.483	0.179	2326	49	37(76%)	3	5	2	2
2	7	487	0.001	0.473	0.173	2339	49	37(76%)	5	4	2	1
3	3	370	0.001	0.347	0.129	2502	50	33(66%)	8	7	2	0

B								Prediction of incidence category				
Model	χ^2 's	P^b	R^{2c}	n^f	Correct	Under 1	Over 1	Under 2	Over 2			
1	9	0.001	0.448	24	19(79%)	3	1	1	0			
2	7	0.001	0.384	24	18(75%)	3	2	1	0			
3	3	0.001	0.405	24	15(62%)	6	3	0	0			

^aModel chi-square

^bStatistical significance of model

^cCoefficient of determination

^dReduction in log-likelihood due to the model

^eBayesian information criterion

^fNumber of observations; differences due to missing values for some variables

The probability of WPBR infection in a tree $[P(Y)]$ was obtained by inserting the test data independent variables into the equation for each model. The equations calculated $\text{logit}(Y)$ (the natural logarithm of the odds of WPBR infection) rather than $P(Y)$ directly. The form of the equation was

$$\text{logit}(Y) = \hat{\beta}_0 + \hat{\beta}_1 \times x_1 + \hat{\beta}_2 \times \hat{\beta}_2 + \dots + \hat{\beta}_k \times x_k$$

where $\text{logit}(Y) = \ln \{P(Y)/[1 - P(Y)]\}$, $\hat{\beta}_0$ is the Y-intercept, x_1 through x_k are the independent variables identified by the stepwise procedure as important predictors of WPBR incidence, and $\hat{\beta}_1$ through $\hat{\beta}_k$ are the coefficients for these independent variables. It was necessary to linearize the predicted value to compare it to the linear observed proportion of trees infected. To accomplish this, $\text{logit}(Y)$ was converted to $\text{odds}(Y)$ by exponentiation, and then to $P(Y)$ by the formula $P(Y) = \text{odds}(Y)/[1 + \text{odds}(Y)]$, where $P(Y)$ is the predicted probability of infection in an individual tree and $\text{odds}(Y)$ is the ratio of the probability that $Y = 1$ to the probability that $Y \neq 1$.

We used least-squares regression to compare the predicted proportion of trees infected with our observed proportion of infected trees and to calculate the significance of the regression and the coefficient of determination. Finally, we assigned the low, medium, and high classes to the predicted and observed values and performed a simple error assessment to see how well the model predicted incidence.

Analysis of the Independent Variables in the Model

To assess the importance of the independent variables, we evaluated the odds ratio, which approximates how much more likely the event (WPBR presence in a tree) becomes with increases or decreases in the value of each independent variable (SAS 1996). We also used the standardized logistic regression coefficients to evaluate the strength of the relationship between each independent variable and the dependent variable (Menard 1995).

RESULTS

Model Development and Validation

The stepwise logistic regression identified 13 variables that were potentially related to WPBR infection. We used these to develop 3 candidate models. For the 1st model we removed 4 variables that were highly correlated ($r > 0.6$) or that were not significant ($P > 0.05$). We created the 2nd model by removing the variables with Wald- χ^2 values < 20 . The 3rd model contained only the 3 variables that stood apart from the others because of their very high Wald- χ^2 values (> 100). Fit statistics, significance, and predictive efficiency for the 3 models are shown in Table 2A.

When applied to the validation set, all 3 regression models were statistically significant ($P \leq 0.001$). The coefficient of determination (r^2) for the models ranged from 0.38 to 0.45.

The level of classification accuracy was highest for model 1, which correctly classified 79.2% of the cases. Model 3 correctly classified 62.5% of the test cases and had a higher r^2 than model 2 (Table 2B).

Importance of Independent Variables in the Model

The most important variables in all 3 models were elevation, mean summer precipitation, and average DBH. Although other variables were also statistically significant, when combined, these variables accounted for a much smaller proportion of the variation in WPBR incidence than the first 3 variables. Table 1 lists the parameter estimates for the variables in each model.

DISCUSSION

Interpretation of Independent Variable Selection

ELEVATION.—In Yellowstone National Park, Berg et al. (1975) reported that WPBR incidence in *Pinus albicaulis* and *Pinus flexilis* decreased with elevation. These researchers found that 92% of all infections occurred below 2591 m (8500 ft) elevation. Our results suggest a similar negative relationship between elevation and WPBR incidence. We found that 97% of the sample stands below 2591 m had WPBR, while only 53% of the stands above 2591 m were infected. However, the average proportion of trees infected in these stands did not decrease with elevation. In fact, the proportion of high-infection sites above 2591 m, 33%, was slightly greater than the proportion of high-infection sites below this elevation, 31%, suggesting that once WPBR is able to infect a high-elevation site, it is able to continue to intensify. However, this phenomenon was apparent only in the Greater Yellowstone Ecosystem portion of our study area. Some factors involved in the decrease in WPBR incidence with increasing elevation may include earlier *Ribes* leaf senescence, cooler temperatures at key times of development or spore dispersal, less susceptible *Ribes* species, or a less favorable spatial pattern of hosts at higher elevations.

PRECIPITATION.—Mean summer precipitation was an important predictor variable in our model. Other researchers have observed a relationship between WPBR incidence and

regional moisture characteristics. For example, Van Arsdel et al. (1956) attributed low WPBR incidence in southwestern Wisconsin to the dry climate of the region.

Optimal temperature and moisture conditions for survival of *Cronartium ribicola* have been well documented (Mielke 1943, Van Arsdel et al. 1956). Infection of pines requires extended periods of time (Charlton 1963) during late summer and early autumn with nighttime temperatures below 19.4°C (67°F) and free moisture on the needle surfaces (Kimmey and Wagener 1961). Van Arsdel et al. (1956) concluded that at least 2 consecutive days of these favorable conditions are required for infection of pines.

Extended temperature data from high-elevation weather stations within our study area were not available, and interpolating temperatures between low-elevation weather stations is inappropriate because of local temperature inversions that are common in mountain environments (Baker 1944). Thus, we did not include a temperature variable in our analysis. We were also unable to locate climate data for mountainous areas that included summer moisture estimates other than mean precipitation amounts. It is generally thought that moist summers are conducive to WPBR development and spread; however, mean summer precipitation alone is probably not the best indicator of favorable climate conditions. For example, Mielke (1943) noted that a heavy “flare up” of WPBR incidence occurred in Idaho during a summer of relatively low mean precipitation in 1937. In fact, dew may be an equally important source of moisture (Mielke 1943). Cloudy summer periods and high relative humidity periods may be better indicators of WPBR incidence than precipitation.

AVERAGE TREE DIAMETER.—The importance of average tree diameter at breast height (DBH) in the logistic regression model may be due to 2 factors. First, smaller-diameter trees tend to have less foliage than larger-diameter trees and are therefore smaller targets for spores. Second, most cankers we inspected were in the upper portion of tree crowns in the interior of stands or throughout the crown of trees on an open edge of the stand. We speculate that wind patterns during times of basidiospore dispersal from *Ribes* to pines concentrate infections along the windward and upper sides of a stand. Wind-dampening effects of

the forest canopy and screening of spores by larger trees may reduce the transfer of spores to smaller, more sheltered trees.

While diameter could reflect the length of exposure, the length of exposure is probably not important because even the smallest trees in our samples likely pre-date WPBR presence in the region.

Average DBH appears to be more important to the intensity of infection on sites that are infected than to WPBR incidence. Of 16 stands with an average DBH of <10 cm, all but 2 were infected, with an average infection level of 19.5% (2–85%) for the infected stands. Of 14 stands with ≥ 20 cm average DBH, 4 were uninfected, and the average infection rate for the infected stands was 46.3% (2–87%).

OTHER VARIABLES.—Other variables were statistically significant in the stepwise logistic regression analysis. However, these variables had much lower Wald- χ^2 values and contributed proportionally much less to explaining observed variability in incidence than elevation, mean summer precipitation, and average tree diameter. Due to the low Wald- χ^2 values and potential correlations between these variables, their statistical and biological significance is suspect. Also, since we did not test each of the independent variables, it is possible that we included irrelevant variables in the model.

Implications for Future Research

The potential relationships between site and stand characteristics that we identified in this analysis represent a “snapshot” in time for the current stage of the developing WPBR epidemic in our study area. These relationships help identify areas where WPBR will likely spread and/or intensify first. Aging cankers could help researchers (1) determine how WPBR has moved and intensified in the region and (2) differentiate between sites susceptible to long-range transmission and those where WPBR intensifies quickly. Such a study could also help researchers predict future spread and intensification of WPBR in the region. However, the characteristics of spread and intensification may change in the future due to genetic adaptations by *Cronartium ribicola*, an exponential increase in inoculum availability, changes in host distributions, or shifts in regional climate patterns.

Management Implications

The ability to identify areas of potential rapid intensification or areas with a low probability of infection or intensification over time would help land managers direct mitigation efforts. For example, a spatial model that identifies these areas of intensification could aid the ongoing search for phenotypically resistant trees, which are highly visible in severely infected stands. In some areas vegetative competition from *Abies lasiocarpa* (subalpine fir) is as much of a concern as WPBR (Keane et al. 1994). A spatio-temporal WPBR spread and intensification model would help managers decide where treatments to reduce this competition would be effective. Where WPBR intensification probability is low, silviculture and/or prescribed fire could be used to reduce competition and provide regeneration opportunities for white pines. Conversely, conducting these activities in areas with a high probability of WPBR intensification could potentially increase inoculum levels through the regeneration of susceptible white pines or an inadvertent increase in *Ribes* abundance. A predictive model could also help resource planners assess the future effects of white pine mortality on wildlife, water quality and quantity, avalanche activity, and recreation.

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