Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana

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Abstract: In 2003–2004, we examined 8031 whitebark pine (*Pinus albicaulis* Engelm.) trees and 3812 seedling-establishment sites in 170 plots for mortality and incidence of white pine blister rust (*Cronartium ribicola* A. Dietr.). We found blister rust in all but four plots (98%), and 57% of all trees assessed for blister rust were either already dead or showed signs of blister rust infection. Mean percentage of trees infected was highest in the southern Canada–United States border area (∼73%), decreasing to a low in the northern region of Banff National Park, Alberta (∼16%), and then rising (∼60%) in the northern end of the study area in Jasper National Park, Alberta. Stands with higher infection, mortality, and canopy kill of trees and higher presence of rust on seedlings tended to be located on the western side of the Continental Divide. In the eight stands in Waterton Lakes National Park, Alberta, that had been previously assessed in 1996, infection levels increased from 43% to 71%, and mortality increased from 26% to 61%, whereas no change was apparent in Glacier National Park, Montana, stands. The impacts of high mortality and infection levels, high crown kill, and reduced regeneration potential, suggest that the long-term persistence of whitebark pine in the southern part of the study area is in jeopardy.

Résumé : En 2003–2004, nous avons étudié l'incidence de la rouille vésiculeuse du pin blanc (*Cronartium ribicola* A. Dietr et la mortalité causée par cette maladie en examinant 8031 arbres (*Pinus albicaulis* Engelm.) et 3812 semis dans 170 placettes. La rouille vésiculeuse était présente dans toutes les placettes sauf quatre (98 %) et 57 % de tous les arbres examinés étaient soit déjà morts ou montraient des signes d'infection. Le pourcentage moyen d'arbres infectés était le plus élevé (∼73 %) au sud dans la région frontalière entre le Canada et les États-Unis, atteignait le minimum (∼16 %) vers le nord dans la région du parc national de Banff et augmentait ensuite (∼60 %) à la limite nord de la zone d'étude dans le parc national de Jasper. Les peuplements où l'infection était plus sévère et la mortalité plus élevée, où il y avait plus d'arbres dominants dont la cime avait été tuée et où la rouille était plus fréquente sur les semis avaient tendance à être localisés du côté ouest de la ligne de partage des eaux. Dans les huit peuplements du parc national des lacs Waterton qui avaient déjà été évalués en 1996, les niveaux d'infection et la mortalité avaient augmenté de respectivement 43 % à 71 % et de 26 % à 61 % tandis qu'aucun changement n'était apparu dans les peuplements du parc national Glacier. L'impact des niveaux élevés d'infection, de mortalité et de cimes mortes ainsi que la réduction du potentiel de régénération indique que la persistance à long terme du pin à écorce blanche dans la partie sud de la zone d'étude est menacée.

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Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is an important component of subalpine ecosystems throughout the higher mountains of western North America, ranging from 107°W westward to 128°W and from just over 55°N southward to 37°N (McCaughey and Schmidt 2001). Within the Rocky Mountains of Canada and the northern United States, white-bark pine ranges from about the Salt River and Wind River ranges in western Wyoming (41°N) north to the area of McBride, British Columbia (53°N), 150 km northwest of Jasper, Alberta (Ogilvie 1990; McCaughey and Schmidt 2001).

The large, nutritious seeds of this keystone species provide an important food source for many animal species including red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), grizzly bears (*Ursus arctos* Linnaeus, 1758), and black bears (*Ursus americanus* Pallas, 1780), many small mammals and birds, and most significantly, Clark's nut-

cracker (*Nucifraga columbiana* (Wilson, 1811)) (Tomback 1982; Arno 1986; Tomback and Kendall 2001). In the Rocky Mountains, whitebark pine also plays an important role in community development following both landscape-scale and local disturbances by facilitating succession on dry, cold, exposed sites, where harsh conditions slow revegetation by other tree species (Callaway 1998; Tomback et al. 2001*b*). It also plays an important role in watershed protection by retaining snowpack and, thus, lengthening the snowmelt period and aiding soil stability. It is a relatively shade-intolerant species, and regeneration opportunities naturally occur through avalanche, glacial retreat, and most commonly, fire (Tomback et al. 2001*a*). At higher elevations, whitebark pine forms stable communities that may persist for ≥1000 years.

However, whitebark pine is rapidly declining throughout the southern distribution of its range, where it is threatened by a number of human-caused and natural factors. These include fire exclusion and resulting competitive replacement by more shade-tolerant tree species, in particular subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.); mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902; MPB); global climate change (Tomback et al. 2001*a*); and white pine blister rust (*Cronartium ribicola* A. Dietr.; WPBR), a rust fungus introduced from Europe early last century. Of all these factors, WPBR has the potential for causing local, if not global, extinction of whitebark pine (Kendall and Keane 2001). Of particular concern is the tendency of WPBR to kill the upper, cone-bearing branches before the tree dies, resulting in loss of seed production (Keane et al. 1994). The recent upsurge in MPB infestations is exacerbating the effects of WPBR and complicating local efforts to restore whitebark pine ecosystems (Tomback and Achuff 2008).

Previous assessments in the Rocky Mountains of northwestern Montana and southern Canada (the Waterton–Glacier International Peace Park) showed that an average of 25%–50% of all whitebark pine trees were already dead, and 80%–100% of the live trees per stand were infected with WPBR (Kendall and Keane 2001). More recent studies in east-central British Columbia west of the Continental Divide (Divide) (Stuart-Smith 1998; Campbell and Antos 2000; Zeglen 2002) showed lower mortality levels and generally lower infection levels than in the southeastern part of the province. Increased concern about the ecological consequences of WPBR infection led to an evaluation of the health of whitebark pine throughout its range in the northern Rocky Mountains.[3] Data on the decline of whitebark pine is critical for designing and implementing restoration strategies for this ecologically important species.

The purpose of our study was to (*i*) quantify the incidence of WPBR and mortality in whitebark pine throughout the northern extent of whitebark pine range in the Rockies, (*ii*) examine whether whitebark pine tree mortality and WPBR infection levels depend on geographical location or tree size, (*iii*) examine whether WPBR infection levels on whitebark pine seedlings depends on geographical location, and (*iv*) quantify the rate of change in WPBR infection and mortality in whitebark pine by resurveying stands assessed in 1995–1997 in the Waterton–Glacier International Peace Park.

Methods

Study area

The study area extended from the southern end of Glacier National Park, Montana (48°26′N, 113°18′W), to near McBride, British Columbia (53°20′N, 120°08′W), on both sides of the Divide (Fig. 1). Whitebark pine is a major component of high-elevation forests in the southern portion of the study area and becomes a minor component from approximately 50°N through the rest of the Canadian Rockies (Arno and Hoff 1989). In the northern portion of its range, whitebark pine occurs in a closed forest type, where it is codominant in the canopy layer with Engelmann spruce. These stands occur on steep mesic slopes of colluvial and morainal landforms generally in the upper subalpine nearer the timberline, but some stands extend down into the lower subalpine (Achuff 1989). Whitebark pine also occurs in an open mixed-conifer forest with Engelmann spruce, subalpine fir, and lodgepole pine (*Pinus contorta* Doug. ex Loud.), on subxeric, steeply sloping southerly and westerly aspects (Achuff 1989).

Stand selection

Stands in Waterton Lakes National Park (WLNP) and Glacier National Park (GNP) that were originally surveyed between 1995 and 1997 (Kendall et al. 1996; Kendall and Keane 2001) were resampled in 2003. Although the original plots were not permanently marked nor were the trees tagged, we were able to resample within the original stands by using geographical coordinates, plot photographs and azimuths (K.C. Kendall, US Geological Survey, Biological Resources Division, Glacier National Park Field Station, West Glacier, Montana, unpublished data).

In the rest of the study area (including additional sites in WLNP and GNP), stands were identified by searching databases and publications for known occurrences of whitebark pine and relying on knowledge of local scientists. Sample stands were selected west and east of the Divide, in closed forest and open forest (usually near the timberline). Stands that were accessible directly by motor vehicle, then mountain bike or foot, were preferentially selected in that order; helicopter access was used to a very limited extent. Based on these criteria, 170 plots were established in 2003 and 2004 to represent as broad a range of habitats within the study area as possible (Fig. 1).

To assess mortality and infection levels of whitebark pine, we used the relevé approach, where plots are placed within a representative portion of the sample stand "without preconceived bias" (Mueller-Dombois and Ellenberg 1974). Representativeness was evaluated based on stand history, vegetation composition, stand structure, aspect, elevation, successional stage, and other ecological attributes (Tomback et al. 2005). Sources of information that identified whitebark pine as a primary or secondary species in stands included the ecological land classifications (ELCs) of the

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[3] B.C. Wilson and G.J. Stuart-Smith. 2002. Whitebark pine conservation for the Canadian Rocky Mountain national parks. Unpublished technical report. Cordilleran Ecological Research, Winlaw, B.C.

Fig. 1. Study area for whitebark pine (*Pinus albicaulis*) survey and level of white pine blister rust (*Cronartium ribicola*, WPBR) infection of whitebark pine in the Rocky Mountains of Alberta, British Columbia, and Montana, 2003–2004. Each circle shows one surveyed plot (*n* = 170). The Continental Divide runs northwest to southeast.
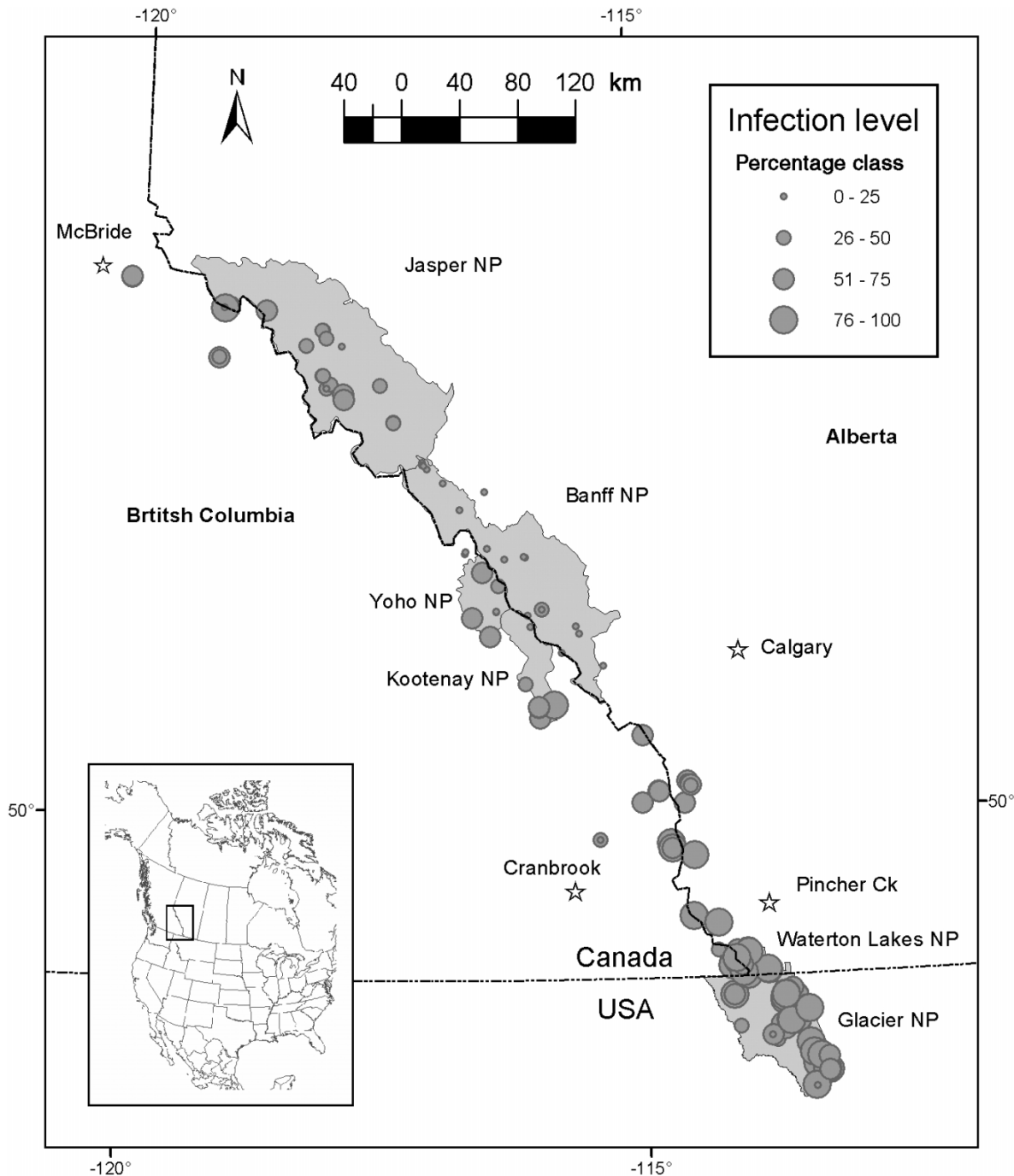
Canadian mountain national parks (Achuff and Corns 1982; Achuff and Dudynsky 1984; Achuff et al. 1993, 2002), provincial forest cover maps (1 : 20 000) and the biogeoclimatic ecological classification (BEC) for British Columbia (Meidinger and Pojar 1991; British Columbia Ministry of Forests 1995).

Survey method

We followed the protocol developed by a multidisciplinary committee of the Whitebark Pine Ecosystem Foundation (Tomback et al. 2005). A 10 m wide belt transect was laid out along an azimuth that avoided changes in aspect, slope steepness, and (or) elevation. The transect was extended to a variable distance that attempted to sample a minimum of 50 whitebark pine trees >1.3 m, with a minimum of 10 trees that were living or recently dead (at least some red or brown needles)[4]. If the transect crossed into another stand type before 50 trees were assessed, then both ends were permanently marked with rebar stakes and a numbered tag, and a GPS location was taken; then, a second transect was placed parallel to the first transect by doubling back, with a 3–5 m gap between transects.

Each tree in the plot was either tagged with a numbered aluminum tag near breast height (or near the base for very small-diameter trees) or mapped by distance along the centre of the transect tape and distance left or right of the tape. In the case of a tree clump (more than one tree growing from an establishment site), each stem that originated below 1.3 m was counted as a separate tree if it could be traced separately to ground level (Zeglen 2002). Whitebark pine trees often grow in clumps because the seeds from which they grow are cached together by Clark's nutcrackers (Linhart and Tomback 1985). This is corroborated by genetic studies that show that the multigenotypic condition of tree clumps arises because the different stems within a clump are separate individuals, having arisen from different trees (Furnier et al. 1987; Rogers et al. 1999). The composition of tree clumps is highly variable, with genetically distinct individuals ranging from 58% to 83% (Tomback and Schuster 1994).

Live trees were visually assessed using binoculars for presence or absence of active or inactive branch and stem cankers caused by WPBR. Active cankers were those that showed diagnostic orange-yellow aecial blisters containing aeciospores in spring or early summer or empty white spore sacs later in the season. Inactive WPBR cankers were identified by their spindle shape, broken bark, and frequent presence of rodent gnawing or bark stripping (Hoff 1992). Diameter at breast height (DBH) to the nearest 0.1 cm, percentage of canopy kill to the nearest 10% (canopy kill indicates the severity of the infection), presence of bark stripping by rodents (showing possibility of WPBR infection), presence or absence of MPB, and tree status (healthy, sick, recently dead (with red needles still attached), or long dead) were also recorded. All dead trees were assessed for the following causes of mortality: WPBR, MPB, and other causes.

All live whitebark pine ≤1.3 m in the plot were considered seedlings and placed in two size-classes (short, ≤50 cm; and tall, >50 cm), and assessed for presence or absence of active or inactive cankers. Both single seedlings and clumps of seedlings were counted as only one seedling site.

Data analyses

We used multiple regression to build five different models for the response of whitebark pine to the same set of topographic predictor variables. The response models were for the percentage of (*i*) live whitebark pine trees with WPBR infection, (*ii*) canopy kill in live trees, (*iii*) dead whitebark pine trees, and (*iv*) tall and (*v*) short seedlings with WPBR infection. For percentages of trees infected with WPBR, the data was normalized through an arcsine square root transformation and analysed using least-squares methods (Sokal and Rohlf 1995). Because the infection data for both seedling classes contained large numbers of zeros, these data were converted to presence or absence of infection and modeled using logistic regression. The common predictor variables were latitude (continuous), Divide (categorical — whether a plot was east or west of the Continental Divide), aspect (the circular aspect data was converted to a linear format, following the trigonometric procedures described in Wilson 2001),

percent slope (continuous), and elevation (continuous). We used forward selection and residual examination procedures described by Nicholls (1989) to select the most parsimonious set of predictor variables and to ensure that the models conformed to the assumptions for each type of analysis. We chose $\alpha = 0.05$ as a criteria to reject terms for model inclusion. Prior to these analyses, we visually explored the data to determine if there were nonlinear relationships between the response and predictor variables that may have been better described by polynomial transformations of the predictor.

We used paired *t* tests to examine differences between infection and mortality levels in the eight stands in WLNP surveyed in 1996 and resurveyed in 2003. We also examined 22 stands in GNP surveyed first between 1995 and 1997 and then resurveyed in 2003. We pooled the first survey years and examined differences between these and the 2003 survey using paired *t* tests. Statistical analyses were performed using S-PLUS 7.0 statistical software (Insightful Corp. Inc. 2005). To analyse seedling density, data were standardized to number of sites per square metre (Tomback et al. 1995).

To eliminate possible biases due to low numbers of trees in a plot, all of the regression models were built using plots with ≥20 live WBP trees (158 plots or 93% of total). However, descriptive analyses included all 170 plots. To further facilitate this description, the surveyed infected and dead trees were grouped into 5 cm diameter classes and reported.

Results

Incidence of WPBR

Over the 2 years of the survey, we completed 170 plots (Fig. 1) and examined a total of 8031 whitebark pine trees >1.3 m in height. The mean number of trees per plot was 47 (median 50, range 4–144) and the mean plot size was 664 m^2 (median 540 m^2, range 140–2830 m^2). Of all plots, 98% had at least one tree infected with WPBR. Of the 8031 trees examined, 90 live trees with heavy lichen loads obscuring the bark were removed from the data set, because they could not be properly assessed for WPBR. Of the resulting 7941 assessed trees, 73% (*n* = 5794) were alive, and 27% (*n* = 2147) were dead. Of the 5794 living trees, 41% (*n* = 2397) were infected with WPBR (had active or inactive cankers). Of these infected trees, 22% had active stem cankers that will likely be lethal within a decade, whereas 24% had only active branch cankers, which may grow down to the stem and become lethal after a decade.

Of the 7941 assessed trees, 80 trees that did not have DBH recorded or were of krummholz growth form were removed from the data set, so analyses involving DBH totalled 7861 trees. The majority of the trees (67%, *n* = 5301) were <15 cm DBH (Fig. 2A). Infection and mortality were spread across all diameter classes (Fig. 2B).

Causes of mortality

Of the 2147 standing dead trees (recently and long dead), we were unable to diagnose the cause of death of 1835 trees

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Fig. 2. Diameter-class distribution of (A) all whitebark pine (*Pinus albicaulis*) and (B) health status of whitebark pine (>1.3 m) by diameter class surveyed across the study area (*n* = 7861). Values above bars are sample size for that diameter class. Trees that did not have diameter recorded (*n* = 80) were removed from the data set for this analysis.
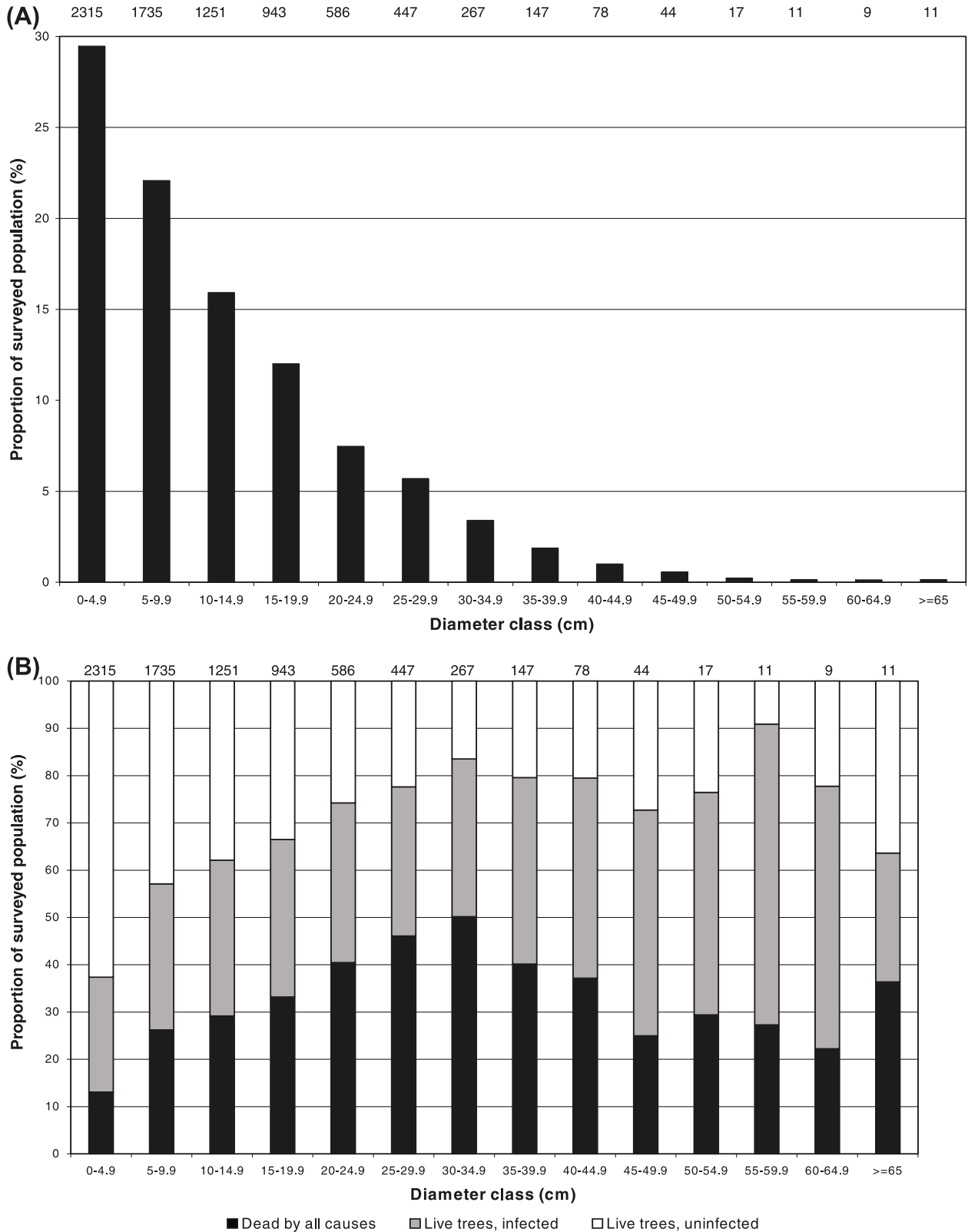
Fig. 3. Effects of latitude and position relative to the Divide for the (A) percentage of live whitebark pine (*Pinus albicaulis*) trees infected with white pine blister rust (*Cronartium ribicola*; WPBR) (plotted lines are third-order polynomial regression curves) and (B) mean percentage of canopy kill in live whitebark pine trees infected with WPBR (plotted lines are second-order polynomial regression curves).
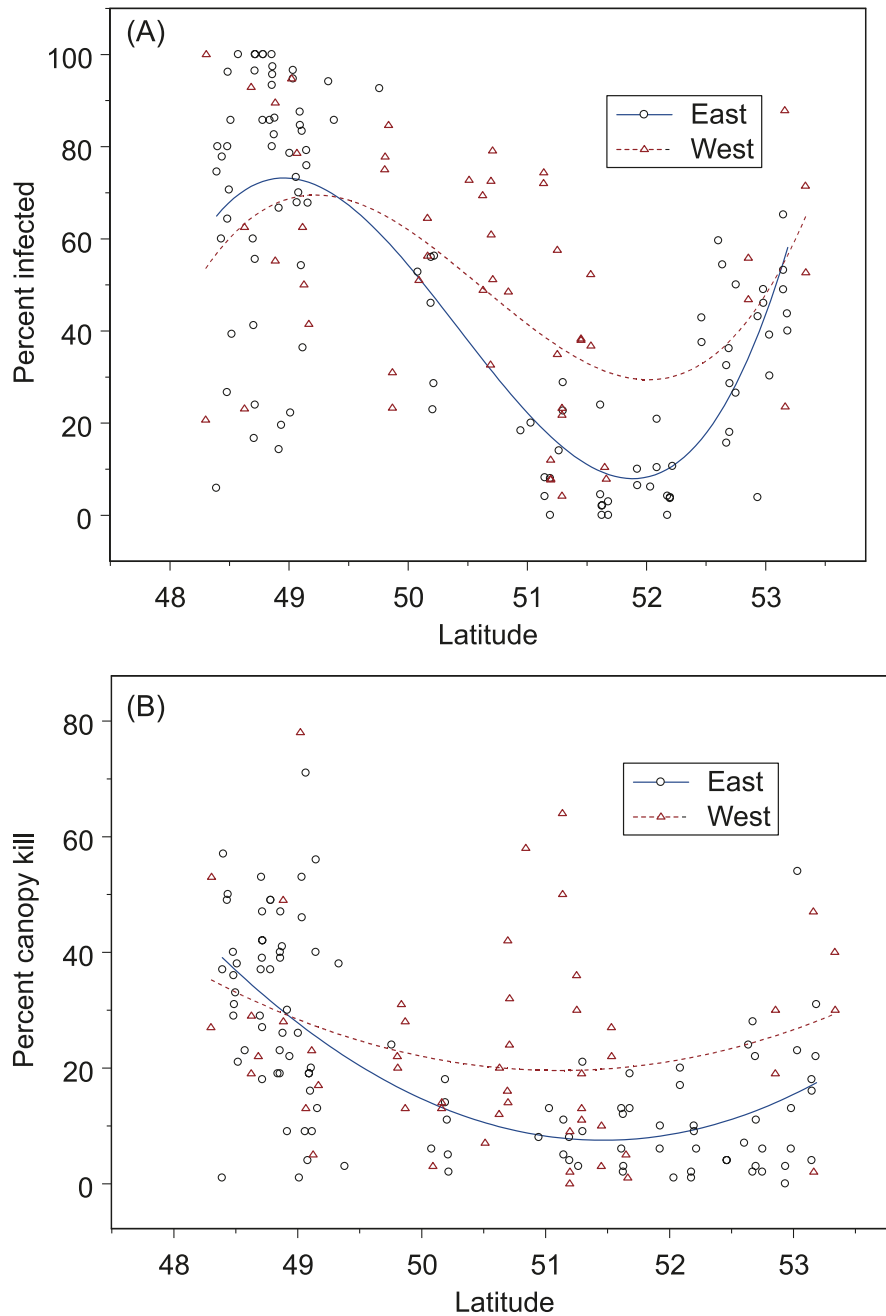
because weathering of the trunks and branches had removed evidence of cankers or beetle galleries. Of the 312 trees for which we could attribute cause of death, 171 (55%) had definite signs of WPBR girdling and evidence of rodent feeding on spermagonial exudate, and 141 (45%) appeared to have died of MPB infestation. Of these 312 trees, 85 were recently dead trees for which we could attribute cause of death: 78 (92%) had definite signs of WPBR, whereas only 7 (8%) had evidence of MPB infestation. Although a small sample size, WPBR appeared to be proportionately more prevalent in smaller diameter trees (mean 10 cm, range 1–

31 cm), whereas MPB appeared to be more prevalent in larger diameter trees (mean 28 cm, range 10–55 cm).

Distribution of mortality and incidence of WPBR

The mean percentage of trees per plot that were infected with WPBR displayed a general wave pattern over the study region (Fig. 3A). The mean percentage was highest in the southern Canada – United States border area (~73%), lowest in the northern region of Banff National Park (~16%), and moderate (~60%) in the northern end of the study area in Jasper National Park and McBride, British Columbia. This

Table 1. Infection, canopy kill, and dead tree models for whitebark pine trees (*Pinus albicaulis*) as shown in Figs. 3A, 4A, and 3B, respectively.

Model and term	df	SS	MS	*F*	*p*
Live tree infection					
Latitude[a]	3	11.21	3.74	50.38	<0.01
Divide	1	0.29	0.29	3.84	0.05
Divide × latitude	3	0.72	0.24	3.23	0.02
Residuals	150	11.13	0.07		
Canopy kill					
Latitude[b]	2	0.01	0.01	26.46	<0.01
Divide	1	0.00	0.00	7.66	0.01
Residuals	154	0.03	0.00		
Dead trees					
Latitude[b]	2	6.81	3.40	124.74	<0.01
Elevation	1	0.37	0.37	13.69	<0.01
Residuals	154	4.20	0.03		

Note: Model R^2 values were 0.52, 0.28, and 0.63 for live tree infection, canopy kill, and dead trees, respectively. SS, sum of squares; MSS, mean sum of squares.

[a]Third-order polynomial.

[b]Second-order polynomial.

pattern was best explained by a third-order polynomial of latitude and accounted for the greatest amount of variation in the response data (Table 1). In the central and northern areas, the stands with higher infection tended to be located on the western side of the Divide, whereas stands to the east of the Divide in the southern regions tended to have higher infection levels. The significance of the interaction between latitude and Divide in the model support this pattern (Table 1).

The mean percentage of canopy kill associated with live trees was highest in the southern region of the study area and lowest in the central region; stands west of the Divide showed significantly higher infection levels (Fig. 3B). This pattern showed some similarity to that of the WPBR infection; however, in this case, 28% of the variance in the data was explained by a second-order polynomial for latitude followed by Divide (Table 1).

Whitebark pine mortality was greatest in southern stands around the Canada–United States border, although there was locally high mortality found in several of the northern stands (Fig. 4A). This latitudinal trend was best described by a second-order polynomial of latitude (Table 1). Elevation was also important in explaining the variance in mortality, and there was decreasing tree mortality with increasing elevation (Fig. 4B). This appears to be more pronounced to the east of the Divide, even though Divide was not a significant descriptor in this model (Table 1). There was minor correlation between latitude and elevation ($r = 0.29$): stands in the southern area had higher mortality at lower elevations.

We sampled 3812 whitebark pine seedlings. Fourteen (8%) of the plots had no seedlings and 12 of these were in the southern part of the study area. Overall, the mean density of the combined seedling size-classes was 0.04 sites/m^2 (range 0–0.45). The distribution pattern of WPBR infection in both seedling size-classes also followed a pattern similar to that seen in the infection of the larger trees (Fig. 5), where a third-order polynomial explained most of the model deviance (Table 2). However, the percentage of infected individuals per plot was reduced sequentially in both the ≤50 cm

and >50 cm classes. Divide appeared to be important in both size-class distributions, whereas the interaction of latitude and Divide appeared only important in the shorter seedling size-class. Both models explained relatively little of the observed variation (>50 cm, 16%; ≤50 cm, 26%).

### Increase in mortality and infection in WLNP and GNP

Among the stands in WLNP, there was a significantly higher incidence of blister rust infection and tree death in 2003 (70% and 61%, respectively) compared with that in the mid-1990s (43% and 26%, respectively). However, there was no difference in either infection or mortality levels in the trees remeasured in GNP compared with when those stands were first surveyed (Fig. 6).

Discussion

The surveys in 2003 and 2004 bring to light two issues. Firstly, WPBR is infecting whitebark pine throughout its range in the northern Rockies from Glacier National Park, Montana, to McBride, British Columbia. Secondly, although mortality and infection levels for the northern and central parts of the study area compare closely to those of previous studies (Kendall et al. 1996; Stuart-Smith 1998; Campbell and Antos 2000; Kendall and Keane 2001; Zeglen 2002), this study shows higher mortality and infection levels of whitebark pine in the southern part of the study area, particularly southeastern British Columbia and southwestern Alberta (Table 3).

The decreasing wave pattern of infection for the trees and seedling classes over higher latitude was essentially the same (Figs. 3A and 5) and may be influenced by a combination of mesoclimatic factors that affect the life cycle and spore dispersal of WPBR (McDonald and Hoff 2001); these include summer precipitation, humidity, growing season length, and fall temperatures (Environment Canada 2006*a*, 2006*b*). However, the higher levels of infection in the southern regions is likely related to the regionally greater abundance of *Ribes* species (Lesica 2002) and the presence of two other regionally occurring primary host tree species:

Fig. 4. (A) Effects of latitude and position relative to the Divide for dead trees (plotted lines are second-order polynomial regression curves) and (B) effects of elevation on dead trees.
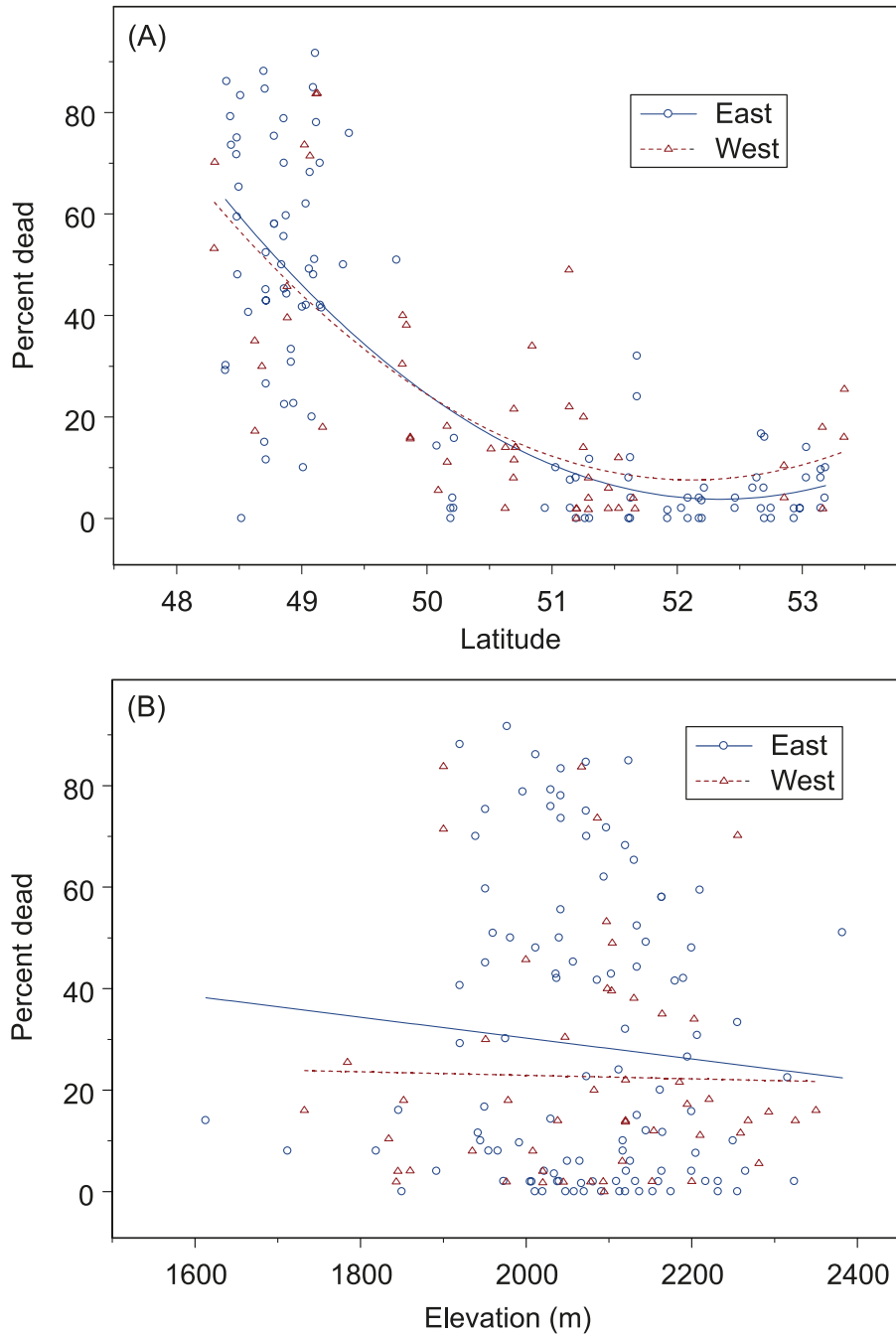
western white pine (*Pinus monticola* Dougl. ex D. Don) (Graham 1990) and limber pine (*Pinus flexilis* James) (Steele 1990). The close proximity of these host species may increase the prevalence of WPBR and, thus, the levels of infection found on whitebark pine in the area compared with areas farther north (Wilson et al. 2002). For example, few *Ribes* and no other host tree species are found in the northern end of Banff National Park (Achuff and Corns 1982) where the WPBR infection is lowest in whitebark pine trees (Fig. 1), whereas western white pine is found in western regions farther south and north.

Although previous studies (Stuart-Smith 1998; Campbell and Antos 2000; Zeglen 2002) observed the south–north decreasing trend, this is the first study to compare mortality and infection levels across the Continental Divide. Both mortality and infection levels in trees showed a tendency to be higher on the west side of the Divide than on the east side, again reflecting the mesoclimatic factors given above with the west side being generally wetter, except for in the southern part of the study area (Environment Canada 2006*a*, 2006*b*). In southwestern Alberta and southeastern British Columbia, the east–west distance across the unvegetated,

Fig. 5. Effects of latitude and position relative to the Divide on the probability of finding live whitebark pine (*Pinus albicaulis*) seedlings infected with white pine blister rust (*Cronartium ribicola*, WPBR) in the (A) >50 cm size-class and (B) the ≤50 cm size-class. The symbols show sites where WPBR is either present (probablity = 1) or absent (probability = 0), and plotted lines are third-order polynomial regression curves.
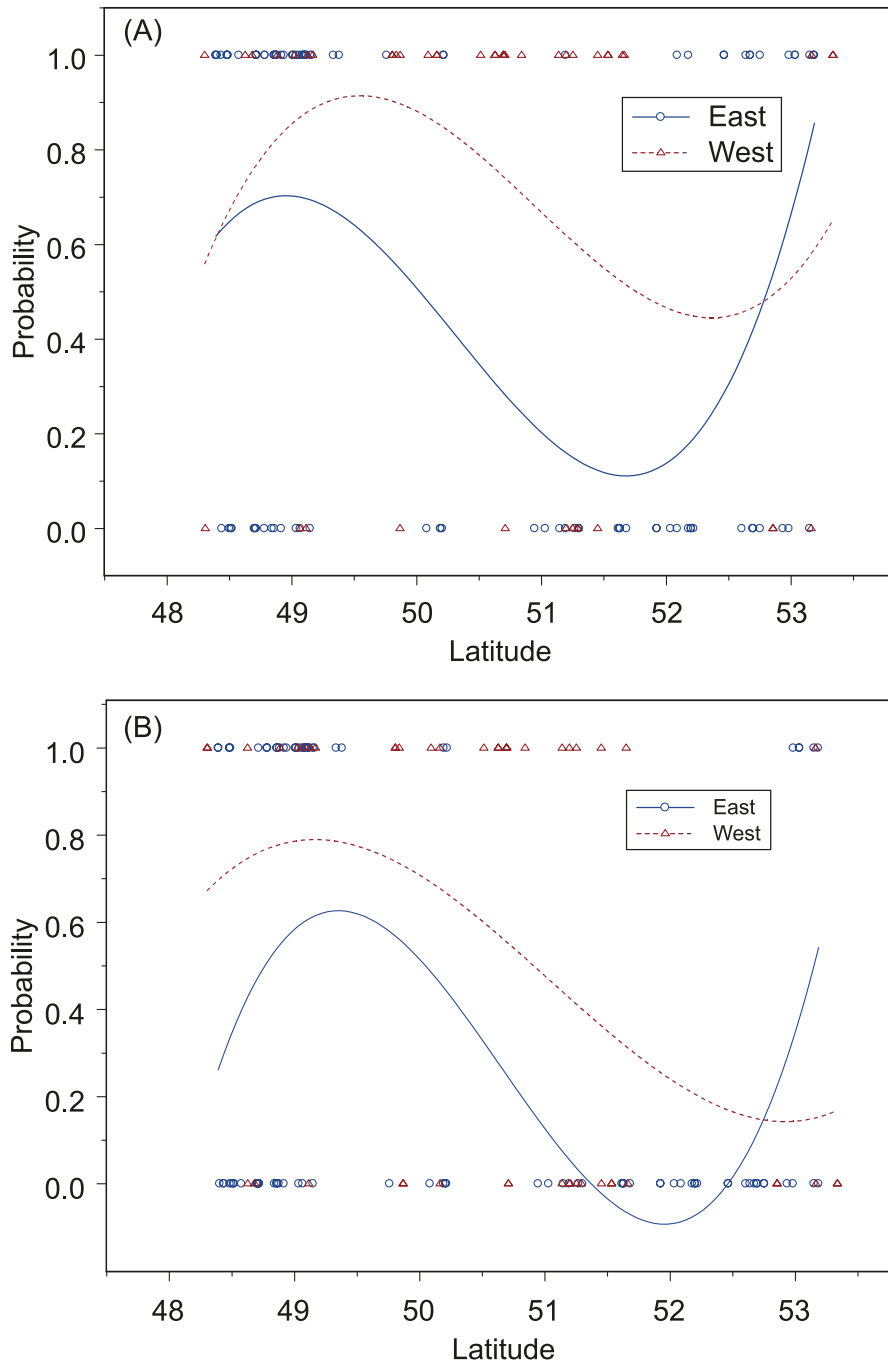
high-elevation portion of the Rocky Mountains is the narrowest in the study area, and climatic differences caused by the Divide (especially precipitation) may be the least pronounced.

One-quarter of the seedlings in the southern part of the study area were infected with WPBR, with decreasing levels further north. The probability of seedlings having WPBR present was slightly higher in taller seedlings. Taller seedlings are generally older and may have had more exposure than younger (shorter) seedlings; also, as seedlings grow, the increased surface area of foliage provides more opportunity for basidiospores to cause infection (Tomback et al. 1995). Seedling mortality was not measured, but experiments by Hoff and Hagle (1990) indicated that, once seedlings develop cankers, the majority die within 3 years. This further reduces the regeneration of whitebark pine forests. Probability of infection in seedlings also showed a decreasing south–north trend.

Table 2. Infection models for tall (>50 cm) and short (≤50 cm) whitebark pine (*Pinus albicaulis*) seedlings as shown in Figs. 5A and 5B.

Model and term	df	Deviance explained (%)	Residual df	Residual deviance	p
Tall seedlings					
Null model			157	215.37	
Latitude[a]	3	20.07	154	195.30	<0.01
Divide	1	7.70	153	187.61	0.01
Short seedlings					
Null model			157	210.76	
Latitude	3	32.62	154	178.14	<0.01
Divide	1	8.43	153	169.71	<0.01
Divide × latitude	3	13.05	150	156.66	<0.01

Note: The tall- and short-seedling models explained 16% and 26% of the deviance, respectively.

[a]Third-order polynomial.

The high level of canopy kill in the southern part of the study area is cause for concern. Nearly all cones are produced in the upper one-third of the crown (Arno and Hoff 1989; Keane et al. 1994), so the loss of canopy means that the potential for cone crops is now very low. Although the trees may be alive, most will have reduced reproductive potential and produce few, if any, more cones in their lifetime; this further reduces opportunities for natural regeneration. The lack of seedlings in 14% of the plots may be an early indication that this is occurring.

Mortality in whitebark pine trees was clearly much higher in the southern portions of the study area (Fig. 4A). Although our ability to attribute cause of death was limited by the amount of weathering of the dead trees, our results suggest that WPBR was the primary mortality agent of whitebark pine in our study area. Evidence of mortality caused by MPB was found primarily in the southern part of the study area, which has a low level of endemic activity but is poised to experience an increase, as well as in Yoho National Park, which has been experiencing exponentially increasing numbers of the beetle since our field work was conducted (Natural Resources Canada 2006). The beetle has been an important agent of mortality in whitebark pine in previous decades. K.C. Kendall (US Geological Survey, Biological Resources Division, Glacier National Park Field Station, West Glacier, Montana, unpublished data) found 40% (78 of 193) of the trees on their plots in WLNP dead from MPB in 1995–1996, the likely result of an epidemic of mountain pine beetle in the late 1970s and early 1980s.[5] It should be noted that stands are more likely to encounter stressors like WPBR spores and MPB at lower elevations where more suitable temperature and humidity conditions are more common. This may help explain the greater mortality seen at lower elevations in this study (Fig. 4B). Logan and Powell (2001) suggest that predicted warmer summer temperatures in the future may allow MPB to more easily invade higher elevation habitats, where whitebark pine becomes an important host. Although MPB prefer larger diameter trees (>10–12 cm) because the thicker phloem layer creates better reproductive conditions (Cole and Amman 1980), even small-diameter whitebark pine trees may be very susceptible to MPB attack because of their proximity to larger diameter stems in multistem clusters (Perkins and Roberts 2003) and because of their proportionately thicker phloem than lodgepole pine of similar diameter (Baker et al. 1971; Waring and Six 2005). Any increased mortality on older, cone-producing trees would further limit opportunities for regeneration of already ravaged forests.

The increasing trend in mortality in WLNP (mortality increased 5%/year calculated over 7 years) (Fig. 6B) is steeper than Keane and Arno's (1993) estimate of 42% over 20 years in western Montana. The increase in infection level in WLNP was 3%/year over 7 years. Although the sample size is small, these trends are of great concern. In WLNP, there has been very low MPB mortality since the early 1980s (Canadian Forest Service, Forest Insect and Disease Survey, unpublished data), so this increased mortality over time may be mostly attributed to WPBR. All of the plots in this study are permanently marked, and the majority have individually marked trees, which will enable continued monitoring of trends in mortality and infection.

The majority of our study plots were in federally protected areas, but our results show that these areas are not immune to global threats. The high mortality and infection levels in the southern part of the study area, the Waterton–Glacier International Peace Park region, suggests that this area is of the highest priority for restoration activities. Not only is the connectivity of these high-elevation ecosystems threatened in this area, but the very persistence of whitebark pine itself on the landscape is in doubt. Ettl and Cottone (2004) modelled the potential for local extinction of whitebark pine in Mount Ranier National Park, Oregon, driven by mortality related to increases in WPBR infection. Using local infection levels that were lower than those observed in the Peace Park area, they concluded that the median time to quasi-extinction (population <100 individuals) was 148 years, less than one generation. Given predicted global climate change, Koteen (2002) highlighted three potential mechanisms that may act singly or cumulatively to reduce whitebark pine in the Greater Yellowstone ecosystem: modified patterns of spread of WPBR (higher elevations), loss of habitat as vegetation shifts upwards in elevation, and changes in species composition as a result of altered fire regimes.

[5]R.A. Watt. 1982. Waterton Lakes National Park: forest damage assessment mountain pine bark beetle, 1982. Unpublished technical report. Waterton Lakes National Park, Waterton Park, Alta.

Fig. 6. Box plots of percentages of (A) live whitebark pine (*Pinus albicaulis*) trees infected with white pine blister rust (*Cronartium ribicola*, WPBR) and (B) dead trees remeasured in permanent plots in Waterton Lakes National Park (WLNP) and Glacier National Park (GNP). The first sampling event occurred between 1995 and 1997, and the second sampling event was in 2003. The shaded areas surrounding the boxes are the 95% CIs. The median value is indicated by the dark line within the 25%–75% quartile box. The *P* values indicate the outcome of paired *t* tests.
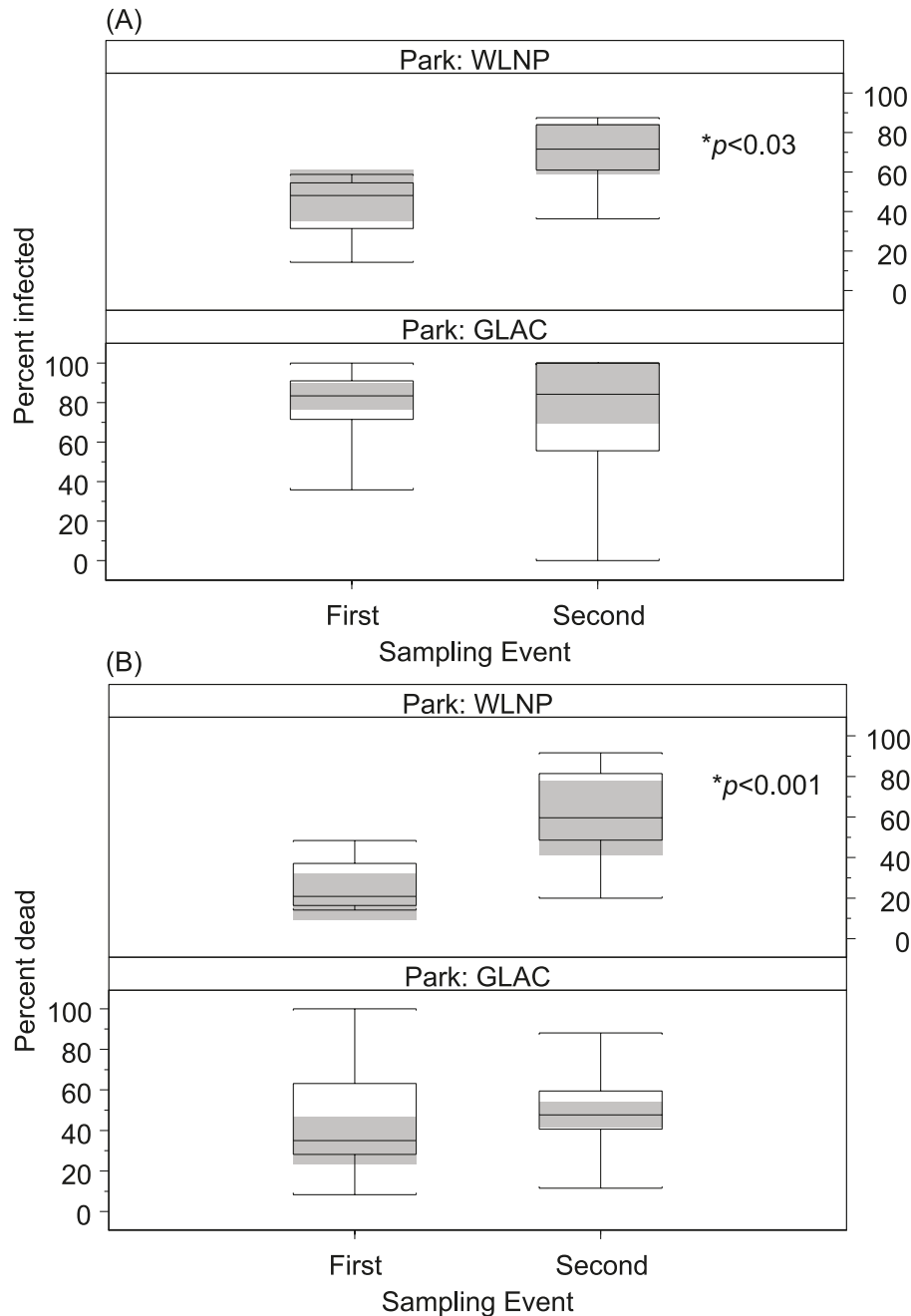
WPBR infection is found throughout the northern extent of whitebark pine distribution, and our stand-level monitoring has shown that infection and mortality rates are increasing over time. The northern Rocky Mountain distribution of whitebark pine is in peril, and the wildlife and vegetation communities that depend on whitebark pine is threatened by the loss of this keystone species, which could trigger a trophic cascade with resultant losses of entire community types and compromised ecosystem function (Tomback and Kendall 2001; Tomback and Achuff 2008). The current combined threats of WPBR and MPB will hasten the loss of whitebark pine and limit any management actions to maintain whitebark pine communities in the future.

Management implications

The data that we present can be used by land managers to prioritize areas for restoration on a landscape scale. For example, the high levels of infection, canopy kill, and mortality and low regeneration in the southern part of this study area suggest a focus of restoration efforts for agencies. Reduced seed availability directly impacts wildlife species, tree regeneration, and potentially the mutualism with seed-

Table 3. Incidence of white pine blister rust (*Tamiasciurus hudsonicus*) and whitebark pine (*Pinus albicaulis*) mortality (for trees >1.3 m in height) for this study and other surveys conducted in the northern Rocky Mountains.

Zone and location	No. of trees	No. of plots	Live infected trees (%)		Dead trees by all causes (%)	Source
			Mean	Range		
Northern						
McBride, British Columbia; Jasper National Park, Alberta	1409	28	42.9	4–88	7.1	This study
Mount Robson area, British Columbia	500		48.3	44–52	13.5	Zeglen 2002
Mount Robson area, British Columbia; Jasper National Park, Alberta	150	7	16.6	0–40	NR	Stuart-Smith 1998
Central						
Yoho and Kootenay National Parks, Elk Pass, British Columbia; Banff National Park, Alberta	2888	56	25.1	0–80	7.9	This study
Yoho and Kootenay National Parks, British Columbia; Banff National Park and Peter Lougheed Provincial Park, Alberta	350	13	16.9	0–56	NR	Stuart-Smith 1998
Southern						
Elk and Flathead valleys, British Columbia	568	12	67.4	41–95	40.6	This study
Cranbrook, British Columbia	2950		44.9		29.9	Zeglen 2002
Cranbrook, British Columbia; southwestern Alberta, Waterton Lakes National Park, Alberta	225	9	59.3	27–76	NR	Stuart-Smith 1998
Waterton Lakes National Park, Alberta	924	15	71.5	22–97	53.3	This study
Waterton Lakes National Park, Alberta	1675	8	44.0	14–59	26.0	Kendall et al. 1996
Glacier National Park, Montana	1954	54	67.0	0–100	46.5	This study
Glacier National Park, Montana	6090	204	78.0	0–100	44.0	Kendall and Keane 2001

Note: NR, not reported.

dispersing birds, such as Clark's nutcrackers (Schoettle and Sniezko 2007). As fewer seeds become available, fewer seeds may be cached, because seed predators such as nutcrackers and red squirrels tend to eat proportionately more seeds when the available seed supply is low (Tomback and Kendall 2001; McKinney and Tomback 2007), thus further reducing opportunities for natural regeneration. Active management, such as supplemental planting of seeds or seedlings, may be necessary to ensure restoration of these forests, even in protected areas. These seeds should only be collected from potentially blister rust resistant trees. These trees might also require protection from MPB attack by using semiochemicals (Kegley and Gibson 2004). Also, the observed trend in mortality in WLNP (e.g., 5%/year increase) provides managers with a sense of urgency associated with restoring whitebark pine. Potentially blister rust resistant trees must be identified, and their seeds must be collected, grown out, and planted in suitable habitats in the shortest possible time.

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