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Changes in white pine blister rust infection and mortality in limber pine over time

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Abstract: Limber pine (*Pinus flexilis* E. James) is under threat from white pine blister rust (WPBR), mountain pine beetle, drought, and fire suppression across its range in western North America. In 2003–2004, we established 85 plots to assess the mortality and incidence of WPBR on limber pine, and remeasured them in 2009. Infection was evident in 74% of the plots in 2003–2004 and 88% of the plots in 2009. The proportion of dead trees increased from 32% in 2003–2004 to 35% in 2009. The percentage of live trees infected increased from 33% in 2003–2004 to 43% in 2009. Mean live limber pine basal area in 2009 ranged from 0.03 to 77.8 m²/ha per plot. Twenty (24%) of the plots had no seedlings in the first measurement, but only 15% in the second measurement. Seedling infection was low (8% in 2003–2004 and 4% in 2009). In 12 plots that were measured three times, mortality increased from 30% of all trees in 1996 to 50% in 2003, then decreased to 46% in 2009. Infection decreased from 73% of live trees in 1996 to 46% in 2003, then increased to 66% in 2009. High mortality and infection levels suggest that the long-term persistence of many limber pine populations in the southern part of the study area are in jeopardy, and continued monitoring is needed to assist with management decisions.

Résumé : Le pin flexible (*Pinus flexilis* E. James) est menacé par la rouille vésiculeuse du pin blanc (RVPB), le dendroctone du pin ponderosa, la sécheresse et la suppression du feu partout dans son aire de répartition dans l'ouest de l'Amérique du Nord. En 2003–2004, nous avons établi 85 placettes pour évaluer la mortalité et l'incidence de la RVPB sur le pin flexible et nous les avons remesurées en 2009. L'infection était évidente dans 74 % des placettes en 2003–2004 et 88 % des placettes en 2009. La proportion des arbres morts a augmenté de 32 % en 2003–2004 à 35 % en 2009. Le pourcentage d'arbres vivants infectés est passé de 33 % en 2003–2004 à 43 % en 2009. La surface terrière moyenne des pins flexibles vivants variait en 2009 de 0,03 à 77,8 m²/ha par placettes. Il n'y n'avait aucun semis dans 24 % des placettes lors de la première mesure contre seulement 15 % lors de la seconde mesure. Le taux d'infection des semis était faible (8 % en 2003–2004 et 4 % en 2009). Dans 12 placettes remesurées trois fois, la mortalité est passée de 30 % de tous les arbres en 1996 à 50 % en 2003 puis a diminué à 46 % en 2009. Le taux d'infection est passé de 73 % des arbres vivants en 1996 à 46 % en 2003 puis a augmenté à 66 % en 2009. Les taux élevés d'infection et de mortalité indiquent que la persistance à long terme de plusieurs populations de pin flexible dans la partie sud de la zone d'étude est menacée et qu'un suivi continu est nécessaire pour faciliter les décisions d'aménagement. [Traduit par la Rédaction]

Introduction

Limber pine (*Pinus flexilis* E. James) is a five-needled white pine that ranges from southwestern Alberta and southeastern British Columbia, south to New Mexico, Arizona, and eastern California, with notable outlying populations in North Dakota, South Dakota, Nebraska, eastern Oregon, and southern California (Steele 1990). It grows across a broad range of elevations from lower to upper tree line, in a broad array of habitat types (Webster and Johnson 2000). It frequently grows on exposed and wind-swept sites where its tolerance to exposure and drought confers a competitive advantage over other less-tolerant conifers, which often out-compete limber pine on productive sites (Schoettle 2004b).

Limber pine plays important roles in the harsh environments in which it lives, including colonizing disturbed areas (Donnegan and Rebertus 1999), retaining snowpack, protracting snowmelt, and acting as nurse trees providing shade and protection for other plants (Baumeister and Callaway 2006). Limber pine cones open in late August to early September when they become mature (Benkman et al. 1984). Its large wingless seeds are a high-energy food source for many mammal species, including red squirrel (*Tamiasciurus hudsonicus* Erxleben, 1777) (Hutchins and Lanner 1982), black bear (*Ursus americanus* Pallas, 1780) (McCutchen 1996),

and grizzly bear (*Ursus arctos* Linnaeus, 1758) (Kendall 1983); and a host of bird species, such as Clark's nutcracker (*Nucifraga columbiana* Wilson, 1811) (Benkman et al. 1984; Schoettle and Negron 2001). Clark's nutcrackers store seeds in the ground for later use, and uncollected seeds may germinate and grow into trees (Lanner and Vander Wall 1980; Tomback and Linhart 1990).

Limber pine populations, particularly in the central and northern parts of the range, are threatened primarily by white pine blister rust (WPBR), caused by the non-native fungus *Cronartium ribicola* J. C. Fisch. (Schoettle et al. 2008b; Burns et al. 2011; Klutsch et al. 2011), and mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins, 1902) (Langor et al. 1989; Bentz et al. 2011), but also by drought (Kendall et al. 1996; Achuff 1997; Millar et al. 2007) and fire suppression (Schoettle 2004a, 2004b). While each of these factors individually pose significant threats to limber pine, together they interact to further increase the severity of the impacts. Furthermore, climate change and associated change in environmental conditions (e.g., temperature and precipitation), is likely to exacerbate the challenges already threatening limber pine (Schoettle et al. 2008a).

WPBR has a complex life cycle, composed of five kinds of spores and two hosts, that takes several years to complete. Two spore stages are produced on five-needled pines and three on alternate

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hosts of the genus *Ribes* (McDonald and Hoff 2001) or less commonly *Pedicularis* and *Castilleja* in the Orobanchaceae (McDonald et al. 2006; Zambino et al. 2007). Each spore stage has very strict conditions of temperature and humidity under which infection occurs, resulting in "wave years" of high infection rate when these conditions are just right (McDonald and Hoff 2001). WPBR impacts limber pine not only through tree and branch mortality, but also by reducing seed availability, seed dispersal, and seedling survival (Schoettle 2004b). As the rust spreads through the phloem, the nutrient supply can be cut off to the branches or stem, or rodents may feed on the vascular canker tissue, usually resulting in girdling of the branch or stem, causing branch or tree death (Hoff 1992). The death of cone-bearing branches (canopy kill) results in fewer and often smaller cones, and overall reduced seed production (D.W. Langor, unpublished data). When fewer cones and seeds are available, there is a reduced likelihood that nutcrackers will visit a stand to forage, ultimately reducing seed dispersal (McKinney et al. 2009). Limber pine seedlings are also susceptible to WPBR infection, and seedling mortality is common in many infected stands. In a greenhouse trial of seedling susceptibility to WPBR, Hoff and McDonald (1993) found that limber pine seedlings had three times the level of infection than those of whitebark pine (*Pinus albicaulis* Engelm.) seedlings. Most seedlings die within 1–3 years after infection (Schoettle and Sniezko 2007).

WPBR was accidentally introduced to Canada's west coast from Eurasia in the early 20th century (McDonald and Hoff 2001) and spread eastward to Alberta, where it was first identified on limber pine in 1952 (Gautreau 1963). Within a decade, it had caused heavy infection and mortality in an unspecified number of sample plots in southwestern Alberta (Gautreau 1963). By 1996, high infection levels (range 43%–96%) and mortality from multiple causes (range 5%–57%) were reported (Smith et al. (2011a), revised from Kendall et al. (1996)). The continuing spread and impact of WPBR (ASRD and ACA 2007) resulted in limber pine being listed as "Endangered" under *The Wildlife Act* in Alberta in 2008 (Government of Alberta 2010). WPBR has now spread throughout nearly the entire range of limber pine in North America (Schwandt et al. 2010). Risk assessments of many currently healthy areas (e.g., parts of Colorado and New Mexico, the Great Basin, and southern California) conclude that limber pine there are threatened by WPBR, as conditions are appropriate to support the fungus as it continues to spread (Howell et al. 2006; Burns et al. 2008).

Several studies (Kearns and Jacobi 2007; Kliejunas and Dunlap 2007; Jackson et al. 2010; Burns et al. 2011) have reported on the incidence of WPBR on limber pine and subsequent mortality, but none have reported on rates of change in these parameters. Both infection and mortality, and their rates of change, may vary at different stages of an epidemic or be affected by stand age, environmental conditions, and other factors. Thus, it is important to examine how stands and landscapes respond over time, to provide metrics for parameter estimations for models specific to the five-needle pines (e.g., Field et al. 2012), and to inform management and recovery actions for limber pine (Geils and Vogler 2011).

Thus, the objectives of this study were to (*i*) document the incidence of WPBR and mortality in limber pine and (*ii*) determine how infection and mortality rates from WPBR are changing over time and across geographical gradients. We then apply the results to highlight implications for management of limber pine.

Methods

Study area

The study area (Fig. 1) extended across most of the range of limber pine in Canada, predominantly on the east side of the Continental Divide from Waterton Lakes National Park, Alberta (49°0′N, 114°2′W), to west of Nordegg, Alberta (52°16′N, 116°23′W), with two plots west of the Continental Divide as far as Golden, British Columbia (51°18′N, 116°54′W). Limber pine is a major com-

ponent of low- and mid-elevation forests on xeric to sub-xeric, exposed and wind-swept ridges in the southern third of the study area, and a minor component of stands farther north (ASRD and ACA 2007). In lower subalpine forests, limber pine may co-occur with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and occasionally whitebark pine. In montane forests, limber pine may also co-occur with Engelmann spruce, lodgepole pine (*Pinus contorta* Doug. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and white spruce (*Picea glauca* (Moench) Voss) (Achuff 1989). In the Porcupine Hills, limber pine commonly grows in open stands in a grassland ecosystem (Archibald et al. 1996).

Stand selection

In southwestern Alberta, 12 stands originally surveyed in 1996 by Kendall et al. (1996) were resampled in 2003. Although few of the original plots were marked and trees were not tagged, we used geographical coordinates, plot photographs, and azimuths to locate the plots again with high confidence within the original stands (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, stands selected for survey were identified by searching databases and publications for known limber pine occurrences and by relying on local knowledge. Sources of information that identified limber pine as a primary or secondary species in stands included the ecological land classifications of the Canadian mountain national parks (Achuff and Corns 1982; Achuff et al. 1993, 2002), provincial forest cover maps (1 : 20 000) and the Biogeoclimatic Ecological Classification for British Columbia (Meidinger and Pojar 1991; British Columbia Ministry of Forests 1995).

To assess mortality and infection levels of limber pine, we used the relevé approach, the cornerstone of which is that plots are placed within a representative portion of the sample stand "without preconceived bias" (Mueller-Dombois and Ellenberg 1974). Representativeness was achieved by choosing stands to include a wide range of attributes, including stand history, vegetation composition, stand structure, aspect, elevation, successional stage, and other ecological attributes (Tomback et al. 2005). Stands that were accessible directly by motor vehicle, mountain bike, or foot were preferentially selected; helicopter access was used to a very limited extent. Based on these criteria, in 2003 and 2004 we re-established the 12 plots from 1996 and established 73 new plots, to represent as broad a range of habitats within the study area as possible (Fig. 1).

Survey methods

The following topographic and stand characteristics were recorded: elevation (m), slope (%), aspect (°), and overstory composition. For the calculation of overstory composition, only live trees over 5 m tall or ≥10 cm diameter at breast height (DBH) were included, and total overstory had to equal 100% for each plot.

Methods for establishing plots and assessing health were adapted from those recommended by Tomback et al. (2005) for whitebark pine (Smith et al. 2008). A 10-m wide belt transect was laid out either along an azimuth that avoided changes in aspect, slope steepness, and (or) elevation, or following the ridge crest if the stand was linear. Tomback et al. (2005) recommended a fixed transect length of 50 m, but our surveys were started in 2003, using a draft of the methodology that recommended a minimum number of live and dead trees rather than a fixed length, which resulted in large plot sizes in stands where mortality was very high or trees were sparse. Starting in 2004, transect length was set at 50 m and most of the 2003 plots were standardized and reduced to 50 m in length when remeasured in 2009. Despite the reduction in area from 2003 to 2009 in many plots, we are comfortable that the limber pine conditions in the smaller plots utilized in 2009

Fig. 1. The study area for the limber pine (*Pinus flexilis*) surveys, the level of white pine blister rust (*Cronartium ribicola*) infection in 2009 (indicated by the size of the circle symbol), and the percentage change in infection between 2003–2004 and 2009 (the colour of the circle symbol) in the Rocky Mountains of Alberta and British Columbia. Each symbol represents one surveyed plot (*n* = 85). Ellipses enclose plots by area as per Tables 1 and 2.
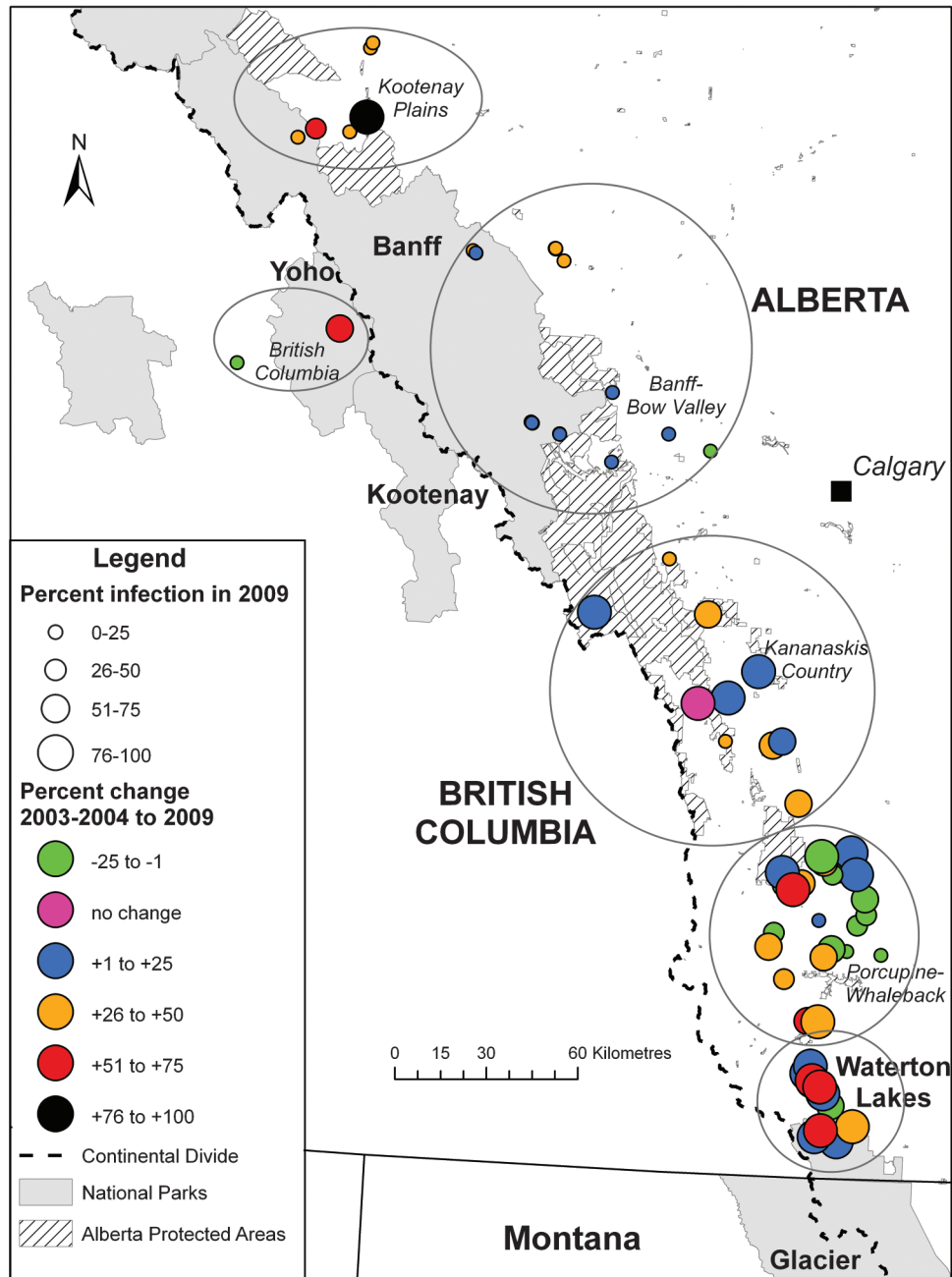
were representative of the larger plots utilized in 2003. All trees within plots on public lands were marked with numbered aluminum tags and only the beginning and end trees of the plot were tagged on private land.

Two growth forms were recognized for limber pine: (*i*) trees with upright stems >1.3 m in height and (*ii*) krummholz, stems that were prostrate and laterally growing, even for individuals of reproductive age. Krummholz individuals were discriminated from seedlings by current or past evidence of cones. Except where otherwise noted, we use "trees" to include both growth forms. In a multistem tree clump, each stem that originated below 1.3 m was counted as an individual if the stem could be traced separately to ground level (Kearns and Jacobi 2007). All live limber pine

≤1.3 m tall (except for the krummholz growth form) were considered seedlings classified in one of two height classes, ≤50 cm and >50 cm, and assessed for the presence of cankers. Both single seedlings and clumps of seedlings were counted as one seedling site. Limber pine often grow in clumps because multiple seeds (from the same or different trees) are cached in one hole by Clark's nutcrackers (Linhart and Tomback 1985), and these different seeds give rise to separate individuals. These clumps can only be distinguished from multiple-trunk trees by genetic studies (Schuster and Mitton 1991; Carsey and Tomback 1994; Feldman et al. 1999). The composition of tree clumps is highly variable, with the proportion of genetically distinct trees ranging from 18% (Schuster and Mitton 1991) to 81% (Carsey and Tomback 1994).

Table 1. Mean (range in parentheses) percent cover of overstory species and topographic characteristics (elevation, slope, and aspect) for 85 limber pine (*Pinus flexilis*) plots.

Area	PF	FD	SE	PL	FS	AT	Elevation (m) (range)	Slope (%) (range)	Aspect (°) (range)
British Columbia	66	34	0	0	0	0	1468 (1460–1475)	35*	260 (250–270)
Kootenay Plains	90	0	10	0	0	0	1425 (1345–1682)	43 (10–70)	171 (140–230)
Banff / Bow Valley	78	4	12	5	1	0	1646 (1228–1958)	42 (17–63)	213 (150–260)
Kananaskis Country	92	2	4	2	0	0	1607 (1310–1964)	34 (20–50)	203 (160–250)
Porcupine/Whaleback	87	13	0	0	0	0	1451 (1220–1712)	25 (10–35)*	240 (110–290)
Waterton Lakes	82	7	1	1	5	4	1686 (1302–1970)	29 (5–65)	174 (20–340)
Mean	**83**	**10**	**4**	**1**	**1**	**1**	**1560**	**35**	**203**

Note: See Fig. 1 for the location of the areas. PF, limber pine (*Pinus flexilis*); FD, Douglas-fir (*Pseudostuga menziesii*); SE, Engelmann spruce (*Picea engelmannii*); PL, lodgepole pine (*Pinus contorta*); FS, subalpine fir (*Abies lasiocarpa*); and AT, trembling aspen (*Populus tremuloides*).

*Some plots were missing percent slope data.

Binoculars were used to assess tall trees for branch and stem cankers caused by WPBR. Active cankers showed either the presence of orange-yellow aecial blisters containing aeciospores (most common in May and early June) or empty white spore sacs later in the season. Inactive cankers were identified by their spindle shape, broken bark, and frequent evidence of gnawing or bark stripping by rodents (Hoff 1992). Infection severity for branch cankers, recorded on 1688 trees on 51 plots in 2003–2004, was based on the distance of the canker from the stem and classified into three categories: within 15 cm, within 60 cm, and >60 cm. For every limber pine tree on each plot the following data were recorded: the DBH (to nearest 0.1 cm), the percentage of canopy killed to the nearest 10% (canopy kill indicates the severity of the infection), the presence of bark stripping by rodents (which can indicate the possible presence of an old canker), the presence of current and past MPB damage, and tree status (healthy, sick, recently dead, or dead). Recently dead trees displayed red or brown needles. Only standing dead trees were counted. Dead trees were assessed for the cause of mortality: WPBR, MPB, unknown, or other causes. Evidence of MPB included old egg galleries in bark or J-shaped galleries in trees with bark missing.

Data analyses

To determine factors that influence infection and mortality rates from WPBR through time and across the study area, we analyzed spatial and temporal patterns of limber pine health on all 85 plots, using four response variables: (*i*) the proportion of live trees with infection, (*ii*) the mean proportion of the canopy killed on each live tree, (*iii*) the proportion of limber pine trees in the plot that were dead, and (*iv*) the proportion of seedlings exhibiting infection.

For the first three variables, data were logit-transformed to yield a normal distribution, and plots with proportions of 0 or 1 were adjusted by adding or subtracting 0.01, respectively. There were no statistically significant correlations among any of the predictor variables at $R < 0.5$. Data from the first three response variables were analyzed using linear regression. Seedling infection data had a large number of zeroes and were therefore analyzed as presence or absence of seedling infection using logistic regression. The predictor variables for all analyses were UTM Northing (included as a quadratic term), elevation (m), and time (year of sampling). In each model, a random intercept for the plot was added to account for repeated measures at the same plots over time. We used the procedures *xtreg* and *xtlogit* in Stata 10.1 (StataCorp 2007) for the analyses.

Incidence of infection by blister rust was reported as proportion of live trees or seedling sites that were infected at the time of each survey (Smith et al. 2011*a*). Tree mortality was attributed to multiple causes (i.e., WPBR, MPB, drought, etc.) or one causal agent (WPBR or MPB), as a proportion of dead trees and only in cases where cause of death could be determined. For the majority of trees, we were unable to determine cause of death because weathering of the trunks and branches removed evidence of rust can-

kers and beetle galleries. As there was little change in DBH between sampling times (unpublished data), we used the data from 2009 to report on diameter class distribution, grouped into 5-cm diameter classes. All individuals with the krummholz growth form, and trees that did not have DBH recorded, were removed from the data set.

Live basal area (BA) was calculated from the DBH of each tree and summed by plot, regional area, and study area (McKinney 2007). Limber pine trees on two plots were entirely of the krummholz growth form and were removed from the data set. To analyse seedling density, data were standardized to the number of seedling sites per square metre (Tomback et al. 1995).

Results

Stand characteristics

Surveyed plots ranged in elevation from 1220 to 1970 m, with a mean elevation of 1560 m. Most plots were on a southwest aspect and the mean slope was 35% (Table 1). Limber pines were found as the sole tree species in the overstory on 29 plots, in association with Douglas-fir on 27 plots, with Engelmann spruce on 23 plots, with lodgepole pine on 12 plots, with sub-alpine fir on 7 plots, and with trembling aspen (*Populus tremuloides* Michx.) on 5 plots. The number of limber pine trees examined was 4676 in 2003–2004 and 4566 in 2009; the decrease was due to the standardization (reduction) of many of the plots to 50 m in length in 2009, which decreased the mean plot size and the number of trees measured (the mean number of trees per plot decreased slightly from 55 to 54). Mean BA of live limber pine trees among all plots was 19.48 m²/ha in 2003–2004 and 21.96 m²/ha in 2009. Mean seedling density among all plots was 0.010 seedling sites/m² in 2003–2004 and 0.015 seedling sites/m² in 2009. Both mean BA of live trees and seedling density generally increased from south to north across the study area (Table 2).

Incidence of infection and mortality

Of all 85 plots, 74% had at least one tree infected with WPBR in 2003–2004, and this rose to 88% in 2009. Of the assessed trees, 68% (*n* = 3185) were alive and 32% (*n* = 1491) were dead (all causes combined) in 2003–2004; 65% (*n* = 2955) were alive and 35% (*n* = 1611) were dead in 2009. Of 70 trees that died between 2003–2004 and 2009 for which cause of death could be determined, 4% were killed by MPB and 96% by WPBR.

In 2003–2004 and 2009, 66 and 72 trees, respectively, were removed from the data set because they could not be properly assessed for the presence of WPBR because of the bark condition, the presence of covering lichen, or other factors. Of the trees remaining in the data set, those infected with WPBR (i.e., had active or inactive cankers) amounted to 33% (*n* = 1037) in 2003–2004, and 43% (*n* = 1195) in 2009, with a range of 0% to 100% per plot. In 2003–2004, 27% of the infected trees had active stem cankers and this increased to 43% in 2009. Branch cankers within 15 cm of the stem, which are highly likely to grow into the stem

Table 2. Mean (range in parentheses) seedlings/m², live trees/ha and live basal area (BA; m²/ha) for limber pine (*Pinus flexilis*) seedlings and trees in 2003–2004 and 2009.

Area	Seedlings/m²		Trees/ha		BA (m²/ha)	
	2003–2004	2009	2003–2004	2009	2003–2004	2009
British Columbia	0.016 (0.004–0.028)	0.018 (0.012–0.024)	0.4 (0.2–0.7)	0.4 (0.2–0.6)	29.3 (27.9–30.8)	27.2 (26.1–28.4)
Kootenay Plains	0.019 (0–0.080)	0.025 (0.004–0.084)	0.7 (0.2–1.7)	0.8 (0.2–1.9)	29.1 (17.1–39.3)	32.6 (15.1–61.1)
Banff / Bow Valley	0.024 (0.004–0.081)	0.039 (0.006–0.135)	1.4 (0.1–4.7)	1.3 (0.1–4.1)	16.5 (0.1–58.4)	18.5 (5.1–77.8)
Kananaskis Country	0.008 (0.002–0.026)	0.007 (0–0.023)	0.8 (0.01–1.6)	0.8 (0.01–1.7)	15.7 (2.2–27.8)	30.7 (3.8–59.0)
Porcupine/Whaleback	0.008 (0–0.066)	0.010 (0–0.070)	0.8 (0.3–2.1)	1.1 (0.1–2.6)	25.1 (6.7–54.2)	29.2 (2.3–74.1)
Waterton Lakes	0.002 (0–0.008)	0.005 (0–0.022)	1.1 (0.01–2.4)	1.1 (0.3–3.0)	13.3 (0.01–69.4)	8.7 (0.03–42.8)

Note: See Fig. 1 for the location of the areas.

and cause tree mortality, affected 12% of the trees assessed for WPBR severity in 2003–2004 (n = 1688). On average, in 2003–2004, 40% of the canopy of live limber pine trees was dead, and this decreased to 15% in 2009.

The proportion of individuals dead from all causes was higher with the krummholz growth form than the tree growth form in both measurements (42% versus 29% in 2003–2004 and 47% versus 33% in 2009). The same pattern was true for WPBR infection levels: 44% versus 31% in 2003–2004 and 66% versus 37% in 2009. The majority of the trees (76%, n = 2806) were < 15 cm DBH (Fig. 2A). There were no significant differences in the distribution of health status by diameter class (Fig. 2B).

In 2003–2004, seedlings were absent in 24% of the plots, and 7% of all seedlings (n = 623) were infected. In 2009, 15% of the plots had no seedlings, and 4% of all seedlings (n = 900) were infected. At both measurement times, infection was higher in tall (>50 cm) seedlings than in short (≤50 cm) seedlings; 8% versus 0% in 2003–2004 and 7% versus 1% in 2009.

Geographical distribution of infection and mortality over time

Among all 85 plots, the effect of the three covariates varied among response variables (Table 3). Live tree infection (overall model R^2 = 0.55, fraction of variance owing to random effect = 0.57) increased over time but was not related to elevation or latitude (Northing). The proportion of the canopy that was dead (overall model R^2 = 0.57, fraction of variance owing to random effect = 0.19) declined over time and with increasing elevation. The proportion of dead trees in the plot declined with latitude (Fig. 3; overall model R^2 = 0.54, fraction of variance owing to random effect = 0.81) and elevation, but increased over time. The presence of infected seedlings marginally increased with latitude, but was not significantly related to the other covariates (overall model log likelihood = –45.1, $\overline{\chi}^2_{01}$ = 27.4 for test of the significance of the random effect, P < 0.001).

In the 12 plots surveyed three times, the mortality of all trees increased from 30% in 1996 to 50% in 2003, then decreased to 46% in 2009. Infection of live trees decreased from 73% in 1996 to 46% in 2003, then increased to 66% in 2009 (Table 4).

Discussion

White pine blister rust is infecting limber pine throughout most of its range in Canada, and the disease is spreading and increasing in incidence and impact. In 2009, 88% of plots showed evidence of infection, an increase of 14% from our first assessment in 2003–2004. Whereas the average WPBR infection level was 43% of live limber pine trees in 2009, it reached 100% on some plots. This average is higher than the blister rust incidence of 30% reported in Colorado, Wyoming, Montana, and North Dakota (Burns et al. 2011), the 15.5% reported in southeastern Wyoming and northern Colorado (Kearns and Jacobi 2007), and the 0% reported in California (Kliejunas and Dunlap 2007), but lower than the 50% reported in Montana (Jackson et al. 2010). Our observed mortality level of 35% from all causes was considerably higher than the 7% reported in Colorado, Wyoming, Montana, and North Dakota

(Burns et al. 2011) or the 5.4% in southeastern Wyoming and northern Colorado (Kearns and Jacobi 2007). However, Kearns and Jacobi (2007) did not count old dead trees, so the mortality reported by them is underestimated. The lower levels of mortality and incidence in limber pine in study areas south of Montana most likely reflects a shorter time of exposure to WPBR (Schwandt et al. 2010).

Although WPBR incidence showed no response to elevation, both mortality and proportion of canopy killed on live trees were negatively correlated with elevation. This could be due to agents such as drought, bark beetles infesting twigs (e.g., *Pityophthorus* spp.), MPB or WPBR, or a combination of these factors being more prevalent at lower elevations. Rust development and spread may be relatively slower at higher elevations owing to the shorter growing season. This may change, however, if predicted temperature increases at higher elevations because of climate warming provide favorable conditions for WPBR to spread more rapidly (Larson 2010). This relationship to elevation may also be influenced by the presence of alternate hosts and varying microclimatic conditions (Kearns and Jacobi 2007).

The high level of active stem cankers and branch cankers within 15 cm of the stem, which are likely to grow into the stem and become lethal within a decade (Kearns et al. 2009), suggests that the number of trees with top kill could increase considerably in the near future. While top-killed trees remain alive, they will lose the most productive cone-producing branches (Steele 1990), resulting in a decrease in seed production.

Many limber pine in the study area occur on exposed rocky ridges or cliffs, where poor soil conditions and high-velocity dessicating winds often reduce plant vigour, leading frequently to the krummholz growth form. The mature krummholz growth form individuals on these sites had higher infection and mortality levels in both sampling periods than trees did. There are several possible reasons for this difference: (*i*) the distance from needles (site of infection) to stem is shorter in krummholz forms; (*ii*) higher wind velocities on the exposed sites where krummholz is most common could lead to increased spore exposure, although this might be offset by their lower profile; (*iii*) there are fewer other trees in these stands to intercept spores; (*iv*) these sites are more drought-prone (e.g., high winds and shallow soils), which stresses individuals (Schoettle and Rochelle 2000) and could increase their vulnerability to pathogens; and (or) (*v*) possible higher humidity within krummholz may buffer microsite conditions and increase spore survival (Resler and Tomback 2008). Further study is needed to investigate topographical and microsite influences on blister rust incidence in limber pine krummholz. The death of limber pine on these often-isolated rocky ridges, where it serves as a nurse tree (Baumeister and Callaway 2006), could cause cascading effects, and with climate warming, conifers could be lost on these effectively treeline sites (Tomback and Resler 2007; Resler and Tomback 2008).

The significant increase in proportion of live limber pine trees infected with WPBR between 2003–2004 and 2009 suggests that the disease is still spreading. Interestingly, while infection levels in the northern part of the study range have increased, mortality

Fig. 2. Diameter class distribution of (A) all limber pine (*Pinus flexilis*) trees (>1.3 m in height) and (B) health status of all limber pine trees by diameter class surveyed in 2009 (*n* = 3722). Values above the bars indicate the number of trees in that diameter class. Individuals with a krummholz growth form and trees that did not have their diameter recorded are not included.
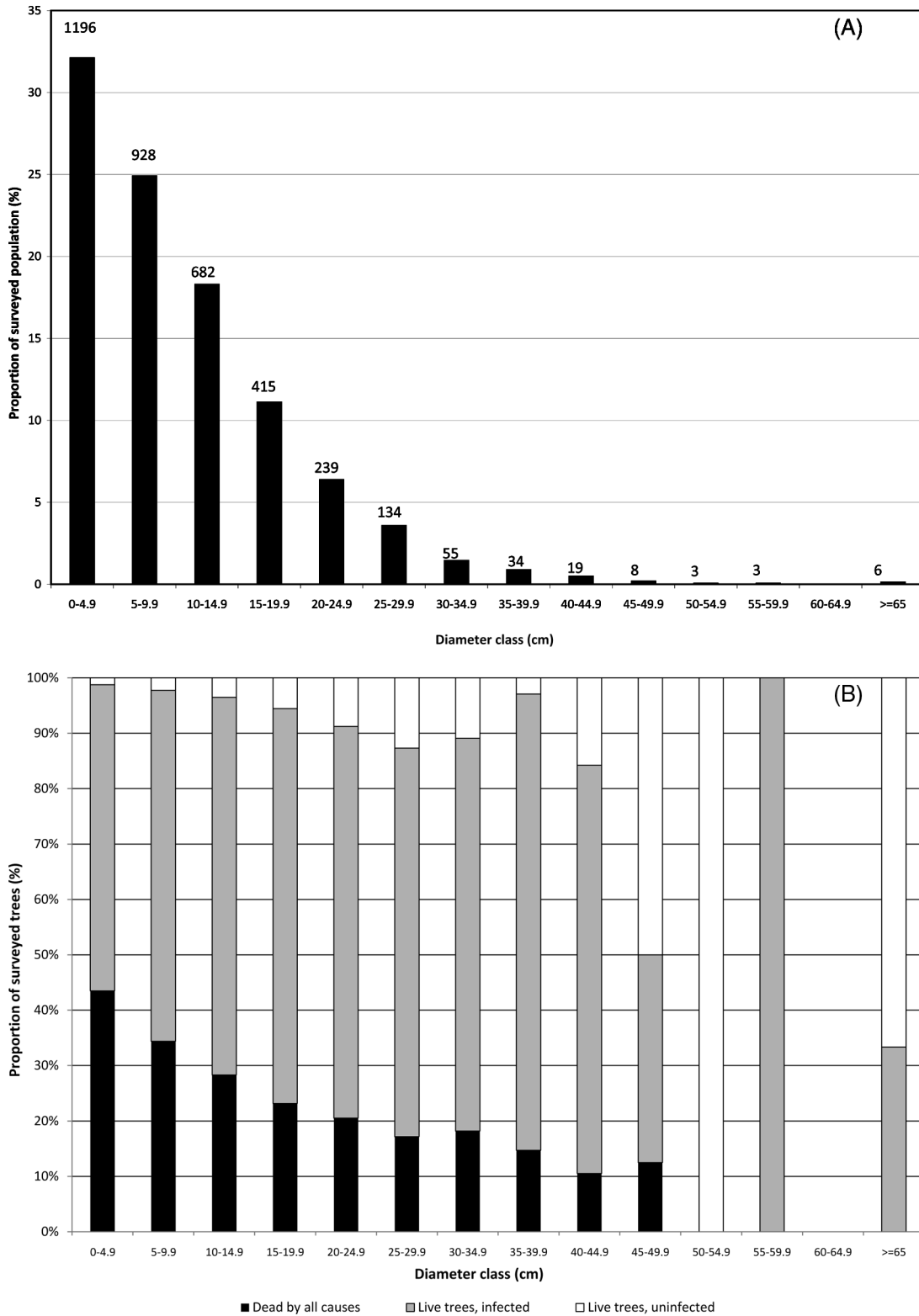
has not, which may indicate (*i*) a higher level of rust resistance in those populations, whereby infection in needles and branches does not progress to the stem and become lethal; (*ii*) it may take longer for the rust to becom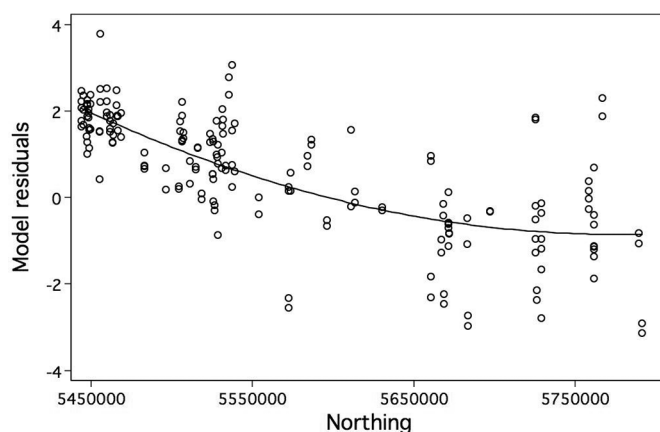e lethal because of climatic influ-ences, such as shorter growing season and colder temperatures; and (or) (*iii*) rodent populations may be lower in the north, which could result in fewer trees killed because of the girdling of in-fected stems. Alternatively, the timing of measurements might

Table 3. Models for the proportion of live limber pine (*Pinus flexilis*) trees (>1.3 m in height and krummholz) with infection, the proportion of live tree canopy killed, the proportion of dead trees, and the presence of infection on seedlings (≤1.3 m in height), including the coefficient for each covariate, its standard error, and the test of its significance.

Model and covariate	Coefficient	SE	p
% Infection live trees			
Northing	0.00002	0.00019	0.909
Northing2	$-3.5e^{-12}$	$1.7e^{-11}$	0.838
Elevation	0.00046	0.00083	0.582
Time	0.084	0.025	0.001
Constant	−184	530	0.728
% Mean canopy kill			
Northing	−0.000029	0.000041	0.472
Northing2	$2.4e^{-12}$	$3.6e^{-12}$	0.506
Elevation	−0.00062	0.00017	<0.001
Time	−0.13	0.010	<0.001
Constant	345	116	0.003
% Dead trees			
Northing	−0.0031	0.00012	0.012
Northing2	$2.6e^{-11}$	$1.1e^{-12}$	0.015
Elevation	−0.0015	0.0005	0.004
Time	0.046	0.010	<0.001
Constant	791	340	0.020
% Seedling infection			
Northing	0.014	0.0074	0.067
Northing2	$-1.2e^{-09}$	$6.7e^{-10}$	0.067
Elevation	0.018	0.012	0.140
Time	0.062	0.159	0.700
Constant	−37973	20720	0.067

Fig. 3. Relationship between the number of dead limber pine (*Pinus flexilis*) trees killed by white pine blister rust (*Cronartium ribicola*) and latitude; highest in the southern part of the study area then decreasing farther north. The model residuals are the residuals after accounting for all the other variables in the model. The solid line is the fitted line using the model coefficients and the means of the other covariates.

Table 4. Incidence of white pine blister rust (WPBR; *Cronartium ribicola*) infection and limber pine (*Pinus flexilis*) mortality in 12 plots in southwestern Alberta for 1996, 2003–2004, and 2009.

Year	Total trees	No. dead	% Dead	No. assessable*	% Live infected
1996	756	226	29.9	530	72.8
2003–2004	977	487	49.8	470	46.2
2009	887	410	46.2	460	65.9

*Live trees that could not be properly assessed for the presence of WPBR because of bark condition, the presence of covering lichen, or other factors were removed from the data set.

Whaleback) to help control this beetle infestation (Alberta Forestry, Lands and Wildlife 1986). The potential for increased mortality of limber pine is high considering that significant MPB populations are still present in southwestern Alberta (Government of Alberta 2012) and outbreaks are projected to increase with warmer temperatures during climate change (Sambaraju et al. 2012).

More of the plots had seedlings in 2009 than in 2003–2004, and the proportion of seedlings infected with WPBR was lower in 2009 than in 2003–2004. The declining proportion of seedlings in the taller height class between measurements suggests that while recruitment is occurring, fewer seedlings are likely to reach reproductive age. However, caution must be exercised when considering seedling infection measurements because the short life span of infected seedlings, and the fact that dead seedlings decompose quickly, means that infected seedlings may have become infected, died, and disappeared between sampling periods and, thus, are not sampled (Field et al. 2012). We did not count dead seedlings in our surveys and the impact of rust on seedlings in our study area is likely underestimated. The higher WPBR infection rate in taller seedlings may simply be related to the higher probability of spores landing on taller seedlings than shorter ones, or that taller seedlings are presumably older than shorter seedlings and, thus, may have had more exposure to spores and (or) their increased foliage surface provided more area for basidiospores to cause infection (Tomback et al. 1995).

The decrease in proportion of canopy in live trees killed by WPBR in live trees over time may be because trees with the highest percentage of canopy mortality in 2003–2004 died by 2009, leaving live trees that were generally healthier. Alternatively, a large infection event may have occurred between measurement years that increased the incidence of WPBR but did not have time to increase canopy loss. Also, this pattern may be explained by infected branches having fallen off and, thus, not being considered in the estimate, or by observer variance in classifying the percentage of canopy kill. Although the percentage of canopy kill declined between measurements, branch death continued to reduce cone production (D.W. Langor, unpublished data), because most cones are produced on main branches in the upper crown (Steele 1990).

Infection incidence and mortality trends among limber pine in the 12 plots over the three measurements were difficult to interpret. There was an increase in mortality of 3%/year between 1996 and 2003, then little new mortality to 2009. The fact that mortality appears to have reached a plateau between the latter two measurements suggests that most of the trees that were susceptible to WPBR had already died and, therefore, only trees with some resistance persisted. This would follow the "natural selection" option of Schoettle and Sniezko (2007), where trees with some resistance are less likely to become infected unless the environment changes in a way that increases their susceptibility or the rust becomes more virulent. The decline in infection incidence on these same plots, from 4%/year between 1996 and 2003 followed by a sharp increase of 3%/year to 2009, could be explained by a wave of new infection (McDonald and Hoff 2001) between the latter two measurements, in which some of the putatively phenotypically

have been between "wave years" and there has not been enough time for the infected trees to die — subsequent measurements will help clarify if this is an important factor.

The majority of limber pine trees killed between 2003–2004 and 2009 for which we could determine cause of death were killed by WPBR. Whereas MPB killed only 7% of trees during this study, an outbreak during the 1980s killed many thousands of limber pine (ASRD and ACA 2007). Over 40 000 trees were also cut and burned north of the Crowsnest Pass (especially in the Porcupine Hills and

disease-resistant trees at the earlier sampling period subsequently succumbed to infection when further exposed. This also demonstrates the importance of long-term monitoring and temporal scale in inferring trends. The presence of a wave year between 2003–2004 and 2009 is also supported by the increase in infection in the <50 cm seedling class. Alternatively, these contradictory rates could in part be explained by varying lengths of time between measurements or the reduction in plot size between measurement periods.

Infection and mortality levels are highest in southwestern Alberta and decrease farther north in our study area (Smith et al. 2011a). A similar pattern of decreasing WPBR infection and mortality with increasing latitude was also found for whitebark pine at the same latitudes (Smith et al. 2008, 2013), a species which suffers from the same threats as limber pine (Tomback and Achuff 2010). This pattern may indicate that there is greater resistance in the populations farther north, that infection is still spreading northward as the fungus spread into Alberta in the south first (Gautreau 1963), or that the probability of infection is being influenced by a combination of climatic, biological, and topographical factors that change with latitude. Mesoclimatic factors, such as summer precipitation, humidity, growing-season length, and (or) fall temperatures, which affect the life cycle and spore dispersal of WPBR (McDonald and Hoff 2001), may vary across the study area. There may also be regional differences in the presence of *Ribes* species (Achuff and Corns 1982) or other alternate hosts (McDonald et al. 2006; Zambino et al. 2007), or in the presence and abundance of additional primary host species such as whitebark pine. The increasingly disjunct distribution of stands of limber pine in the northern part of its range in Alberta (ASRD and ACA 2007) may also reduce the likelihood of individual pines intercepting WPBR spores.

Management implications

Limber pine is a long-lived and slow-growing species that does not produce seeds until 50 or more years of age. It is particularly vulnerable during this prolonged nonreproductive stage. Although limber pine has a wide range, its patchy distribution makes isolated populations vulnerable to extirpation. The presence of two co-occurring significant mortality agents of limber pine, WPBR and MPB, does not bode well for many populations, especially if the beetle kills surviving trees that may be resistant to WPBR. However, patterns of limber pine mortality and infection could be used by land managers to prioritize areas for restoration of the species on a landscape scale. Areas with high levels of WPBR infection and mortality, high canopy kill, and low natural regeneration, such as the southern part of our study area, appear to be a high priority for restoration efforts. At the same time, introducing resistance by planting rust-resistant seedlings into less severely impacted areas, such as the northern part of our study area, may also be advantageous to maintaining self-sustaining populations (Schoettle and Sniezko 2007; Keane and Schoettle 2010; Schoettle et al. 2012). Synergies may be achieved by combining restoration activities with those for whitebark pine (Keane et al. 2012), which is also declining in the study area (Smith et al. 2013).

Limber pine is legally listed as Endangered under *The Wildlife Act* in the Province of Alberta (Government of Alberta 2010), and a recovery strategy is expected in 2013 (B. Jones, co-chair of Whitebark and Limber Pine Recovery Strategy Team, personal communication (2013)) that will likely address priorities for recovery efforts and areas for restoration activities. Protection of limber pine in Alberta may be complicated because many of the stands are outside of protected areas (Fig. 1). The species is blue-listed by the British Columbia Conservation Data Centre, which is similar to "special concern" or "vulnerable" (British Columbia Conservation Data Centre 2012). An unsolicited status report has been submitted to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) for federal assessment (P. Achuff, author of the status report, personal communication (2013)).

The high incidence of WPBR infection and mortality in krummholz growth form limber pine near its elevational maximum in the species' northern range limit may have implications for natural migration as a response to climate warming (Schoettle et al. 2008a; Reinhardt et al. 2011; Moyes et al. 2013). Additional research is warranted, as is continued monitoring of plots and marked trees in this area for status and trends.

Even in the most damaged stands, there were trees that exhibited no infection, or where infection was limited to a few branches, exhibiting putative phenotypical resistance to WPBR. While some efforts are already underway, more seed should be collected from these trees for genetic testing (Schoettle et al. 2011; Sniezko et al. 2011) and restoration planting, and the trees should be protected from MPB (Smith 2009). The decline in limber pine mortality at the northern limit of our study area while infection is still increasing warrants further investigation, as this may indicate some WPBR resistance in these populations. Further investigations could also help us learn more about the environmental influences on wave years. Active management, such as planting of rust-resistant seeds or seedlings (Smith et al. 2011b), will be required to reduce losses of important genotypes, reduce the possibility of local extirpation, and hasten the recovery of this species.

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