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ARTICLE

Hard pine stem rusts on lodgepole pine at a site-preparation study in sub-boreal British Columbia: effects over 24 years

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Abstract: Site preparation can improve lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) survival and growth; however, we lack information regarding possible interactions between treatment effects and the impacts of western gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hirats.) and comandra blister rust (*Cronartium comandrae* Peck). Mechanical and burning techniques examined over 24 years at a sub-boreal British Columbia site did not significantly increase rust infection rates or characteristics relative to an untreated control. Most infection occurred before age 10 years and at heights <2 m. By age 24 years, 22% and 10% of pine had sustained at least one western gall rust or comandra blister rust stem infection, respectively, but only 4% of western gall rust infected trees were dead, compared with 60% of comandra blister rust infected trees. Exploratory regression analysis of the relationship between tree volume and percent stem encirclement and infection height suggested that volume of 24-year-old pine infected with western gall rust averaged 8% less than the corresponding volume of uninfected trees. Over 24 years, estimated stand-level, rust-related volume loss was 8.4%, with the majority due to mortality from comandra blister rust. One-fifth of estimated volume loss was provisionally attributed to growth reductions among live western gall rust infected pine.

Key words: western gall rust, comandra blister rust, lodgepole pine, site preparation, long-term study.

Résumé : La préparation de terrain peut améliorer la survie et la croissance du pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) mais nous manquons d'information concernant les interactions potentielles entre les effets des traitements et les impacts de la rouille-tumeur autonome (*Endocronartium harknessii* (J.P. Moore) Y. Hirats.) et de la rouille-tumeur oblongue (*Cronartium comandrae* Peck). Les méthodes mécaniques et les techniques de brûlage étudiées depuis 24 ans dans une station subboréale de la Colombie-Britannique n'ont pas significativement augmenté les taux d'infection de la rouille ni les caractéristiques relatives au témoin non traité. La plupart des infections sont survenues avant l'âge de 10 ans à des hauteurs <2 m. À l'âge de 24 ans, respectivement 22 % et 10 % des pins avaient été infectés au moins une fois sur le tronc par la rouille-tumeur autonome ou la rouille-tumeur oblongue mais seulement 4 % des arbres infectés par la rouille-tumeur autonome étaient morts comparativement à 60 % des arbres infectés par la rouille-tumeur oblongue. Une analyse de régression exploratoire de la relation entre le volume des arbres, le pourcentage d'encerclement et la hauteur de l'infection a indiqué que le volume des pins âgés de 24 ans et infectés par la rouille-tumeur autonome était en moyenne 8 % plus faible que le volume correspondant des arbres sains. Sur une période de 24 ans, la perte de volume due à la rouille à l'échelle du peuplement a atteint 8,4 %, principalement à cause de la mortalité causée par la rouille-tumeur oblongue. Un cinquième de la perte de volume estimée a été provisoirement attribué aux réductions de croissance chez les pins vivants infectés par la rouille-tumeur autonome. [Traduit par la Rédaction]

Mots-clés : rouille-tumeur autonome, rouille-tumeur oblongue, pin tordu, préparation de terrain, étude à long terme.

1. Introduction

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) is a leading tree species in sub-boreal British Columbia (BC), Canada, and has been widely used to regenerate harvested sites in both North America and Scandinavia (Murray 1983). Numerous studies have shown that early survival and growth of lodgepole pine can be augmented by mechanical site preparation (e.g., Boateng et al. 2012). Whether or not these responses are accompanied by an increased risk of infection by the hard pine stem rusts *Endocronartium harknessii* (J.P. Moore) Y. Hirats. (western gall rust) and *Cronartium comandrae* Peck (comandra blister rust) is unknown. This question is potentially important with regard to early stand management, because the majority of western gall rust and comandra blister rust infection of lodgepole pine occurs by the time trees are 10 years old (Blenis and Li 2005; Henigman et al. 2001), which is also the period when the largest tree response to site preparation occurs (e.g., Boateng et al. 2012). Furthermore, because the responsibility for regenerated stands in BC generally returns from the forest license holder to the government at age 10–15 years, it is important that we possess adequate information to gauge the potential longer term impacts of these pathogens.

Infection of lodgepole pine by western gall rust or comandra blister rust requires specific conditions related to host-tissue

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availability, localized microclimate, and spore production (Adams 1997; Jacobi et al. 2002), and both mechanical site preparation and high-severity fire have the potential to influence these factors in a variety of ways. Because western gall rust primarily infects current-year lodgepole pine tissue (Hopkin et al. 1988), greater availability of susceptible tissue resulting from treatment-related increases in pine leader and lateral shoot growth might be expected to increase rust incidence. Positive correlations between lodgepole pine growth and western gall rust infection have been reported following juvenile spacing in BC (van der Kamp et al. 1995). Similar interpretations regarding the availability of susceptible tissue have been made for other *Pinus* species and stem rust combinations in southern North America (Burton et al 1985) and in Europe (Desprez-Loustau and Wagner 1997). For comandra blister rust, which requires the presence of an alternate herbaceous host (Jacobi et al. 2002), incidence of lodgepole pine infection could be influenced indirectly by the effects of mechanical site preparation or fire on the vegetation community. Finally, sites that are prepared with the objective of enhancing early conifer seedling survival and growth are commonly planted with nursery-grown seedlings. This practice results in a vigorously growing, even-aged juvenile stand, which when very young is highly susceptible to infection (Blenis and Li 2005) during wave years (i.e., years when rust spore release coincides with climate conditions that are ideal for infection (Peterson 1971)).

Interactions between site preparation and damage due to hard pine stem rusts are also important for timber supply projections. Recent modelling exercises based on long-term lodgepole pine responses to site preparation have suggested that growth increases may, in some cases, persist to rotation (e.g., Whitehead et al. 2011). The extent to which these gains might be offset by losses related to mortality and growth reduction caused by hard pine stem rusts is unknown. Possible interactions of site-preparation treatments with hard pine stem rusts notwithstanding, it is critical in this era of widespread losses of mature pine to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and wildfires that timber supply predictions for developing stands are as accurate as possible. To achieve this goal, we need to evaluate the potential losses associated with specific damaging agents such as western gall rust and comandra blister rust (Woods et al. 2010).

Hard pine stem rusts can reduce eventual stand yield through mortality and reduced growth of live infected trees. Comandra blister rust stem infections are nearly always lethal (Hiratsuka et al. 1988), whereas western gall rust stem infections may be present for many years without killing the host pine (Adams 1997). There is a lack of consensus in the literature regarding the degree of mortality that can be expected from western gall rust and even less information regarding potential volume losses in live infected trees. Most efforts at modelling rotation-length volume losses to hard pine stem rusts have focused on mortality and have estimated total losses of between 7% and 15% (Bella and Navratil 1988; Woods et al. 2000). Recent observations have suggested that hard pine stem rust presence in stands that are now 15–25 years old (Heineman et al. 2010; Woods 2011) is higher than would have been expected based on earlier studies (e.g., Nevill et al. 1996). There is concern that this phenomenon could worsen if predicted climate-change effects on annual precipitation patterns become a reality (Spittlehouse 2008; Pike et al. 2010).

As part of a study examining long-term lodgepole pine responses to site preparation in sub-boreal BC (Boateng et al. 2012), western gall rust and comandra blister rust incidence and infection characteristics were recorded over a period of 24 years. In this paper, we seek to answer the following three questions. (*i*) Did mechanical site preparation or high-intensity fire influence rates or severity of infection by western gall rust or comandra blister rust in the 24 year-old lodgepole pine stand? (*ii*) Can we identify treatment-related or other causal factors related either to annual incidence rates of western gall rust or to cumulative infection rates in a stand at the age of 24 years? (Note that we could not address this question for comandra blister rust, because sample sizes were too small and date of infection was uncertain.) (*iii*) What effects did western gall rust and comandra blister rust have on lodgepole pine mortality, growth, and estimated individual-tree and stand-level volume losses at age 24 years?

2. Materials and methods

2.1. Study site

The Bednesti site (53°52′N, 123°29′W) is approximately 50 km west of Prince George, BC, at an elevation of 850 m in the Stuart Dry Warm SBS biogeoclimatic variant (SBSdw3). The ecosystem is characterized by a mean annual temperature of 2.6 °C, mean annual precipitation of 494 mm, mean annual snowfall of 204 cm, and an average of 83 frost-free days per year (Delong et al. 1990). The study site is on gently rolling terrain (0%–10% slope) and is predominantly mesic and of average productivity for the area (Delong et al. 1990). The site was strip harvested in 1963–1964, with remaining strips removed in a second entry in 1971. The site was insufficiently stocked with conifers, and in the winter of 1986–1987, standing trees were knocked down and piled in parallel, regularly distributed windrows using a flat-bladed D8 Caterpillar working on snowpack, with little disturbance to the forest floor.

2.2. Experimental design and treatments

The experiment employed a randomized complete block design consisting of five blocks and five site-preparation treatments: (*i*) mixing of soil with a bedding plow (coarse mixing), (*ii*) disk trenching with pine planted at the hinge of the furrow and the inverted berm material (trench–berm hinge), (*iii*) disk trenching with pine planted in the furrow (trench furrow), (*iv*) burned windrow, and (*v*) untreated except for brush blading (untreated control). In each of the five blocks, the burned windrow treatment was assigned to a single pre-existing windrow and the other treatments were randomly allocated to individual plots ranging in size from 280 to 420 m^2. Site-preparation treatments were applied in fall 1987 and planted with PSB 1+0 lodgepole pine container stock in spring 1988. Forty-eight planted lodgepole pine were assessed in each treatment plot (or windrow), for a total of 240 in each of the five treatments.

2.3. Measurements

From 1988 (after the first growing season) to 1999 (year 12), individual pines were examined for the number of western gall rust or comandra blister rust infections that originated on the stem or on branches (within 10 cm of the stem for western gall rust and within 60 cm of the stem for comandra blister rust). Mortality due to rust infection was also recorded. The rust surveys were conducted in August–September at the same time that tree growth was assessed (Boateng et al. 2012). We acknowledge that the survey timing was not optimal for identifying infections (because young infections are most visible in spring); however, for logistical reasons, it was necessary to collect the rust and tree-growth data simultaneously. From 1988 to 1999, the infection year for western gall rust was assigned by counting live-branch whorls; however, the exact year of infection could not be determined for comandra blister rust, which infects all ages of foliage. In 2010 (year 23), a survey was conducted to locate previously identified western gall rust and comandra blister rust infections. For western gall rust, we confirmed the infection year for previously recorded galls by comparing infection height with annual height-growth data for individual trees. We also recorded current-location status for each of these infections as (*a*) stem (resulting from direct infection of leader tissue), (*b*) indirect stem (resulting from live-branch galls being incorporated into stem tissue), or (*c*) branch. We determined whether individual infections were alive or dead (galls were considered to be dead when they were not in contact with live tree tissue) and recorded the presence of additional stem infections that had occurred since 1999. In a few cases, it was apparent that new galls had developed on older stem tissue. Because these galls could not be accurately aged, they were tallied separately from the annual infection data. For pine that died between 2000 and 2010, mortality cause was assigned based on examination and notations made during previous assessments. In 2011, height to the infection centre (±0.5 cm) and percent stem encirclement were assessed for individual western gall rust and comandra blister rust stem infections on live pine. Percent stem encirclement was calculated from measurements of the stem circumference (±1 cm) and the width of the infection at the widest point (±1 cm) up to a height of approximately 2 m and visually estimated (±5%) above that.

2.4. Climate monitoring

Data were collected from a single climate station at the Bednesti site. With the exception of 1991 and brief periods of malfunction, air temperature and precipitation were measured continuously during 1 May – 30 September from 1988 to 2011 using CR21 (1988), CR10 (1989–1998), and CR10X (1999–2011) dataloggers (Campbell Scientific, Inc.). Air temperature was assessed at a height of 1.3 m using a shielded thermister probe, and precipitation was measured with a tipping-bucket rain gauge. Missing data were replaced (in the case of precipitation) or estimated by linear regression (air temperature) from measurements made at the nearby Vanderhoof Environment Canada weather station (http://climate.weather.gc.ca/advanceSearch/searchHistoricData_e.html). Annual mean daily air temperature, annual mean daily minimum air temperature, and annual total precipitation were calculated from these data for the period of 15 May – 7 July, which is the observed period of spore release for the Bednesti area (R. Reich, unpublished data).

2.5. Data analysis

Cumulative rates of western gall rust infection (i.e., the proportion of lodgepole pine that sustained at least one infection up to the time of assessment, excluding old-tissue infections) were calculated for each year in the period 1988–2011 for two infection locations on the tree, i.e., stem (including indirect infection resulting from live branch galls being incorporated into stem tissue) and branch (≤10 cm from stem), and for the two locations combined. All live and dead trees were included (n = 240 trees·treatment^{-1}; 1200 trees in total). Old-tissue infections (with unknown year of infection) were summarized collectively for 2011. Annual incidence of western gall rust infection of new (leader) tissue on live trees was also calculated for the period 1988–2011. For comandra blister rust, annual incidence of new infections could not be determined due to uncertainty regarding infection year; however, cumulative infection rates were calculated from the total population of live and dead trees to 2011 for stem infections and to 1999 for branch infections.

Univariate analysis of variance (ANOVA) based on a randomized complete block design was used to assess site-preparation treatment effects on percent stem encirclement and height of the largest infection in 2011 (for 3.8% of western gall rust infected pine with two or more infections that had merged into a single mass, the combined mass was considered to be a single infection for the purpose of identifying the largest infection). Sources of variation were random block (B), fixed treatment (T), random B × T (treatment plot), and random tree (nested in plot). The statistical significance of differences between all pairs of treatment means was assessed by the Bonferroni method of multiple comparisons (α = 0.05). Regression analysis was used to examine the relationship between gall age and percent stem encirclement by the largest western gall rust infection. All model residuals were tested for normality, and a corrective ($\log_{10}$) transformation was applied as needed. Treatment effects on the cumulative number of infected trees in a plot, number of infections per tree per plot (including both infected trees (i.e., trees with ≥1 infection) and uninfected trees (i.e., trees with 0 infections)), and number of deaths attributed to (stem) rust disease were analysed in an analogous manner; however, instead of assuming normality, the response variable was assumed to follow either a negative binomial (number of infected trees and number of infections per tree) or a binomial (rust-related deaths) distribution.

Single- and multiple-factor logistic regression analysis was used to examine correlations between annual incidence of western gall rust during the period 1989–2000 (after which no new infections were recorded) and (*a*) 15 May – 7 July climatic factors (precipitation and mean and minimum daily air temperature); (*b*) pine characteristics (height, annual height increment, stem diameter, and age); and (*c*) site-preparation treatment, represented by four indicator variables (1 if a particular treatment was applied and 0 otherwise; all indicators = 0 for the untreated control). The general form of the model (i.e., model 1) was

$$p = \frac{e^{\beta_0+\beta_1 x_1+\ldots+\beta_k x_k}}{1 + e^{\beta_0+\beta_1 x_1+\ldots+\beta_k x_k}}$$

where p is the probability that a leader is infected, $\beta_0, \beta_1, \ldots, \beta_k$ are model parameters to be estimated, and $x_1, \ldots., x_k$ are $k \geq 1$ climatic, pine characteristic, or treatment predictor(s) included in the model. All years between 1989 and 2000 were combined for this analysis. Correlation between infections recorded on successive annual leaders of the same tree were taken into account (together with the other tree characteristics) by inclusion of an indicator of previous infection (1 if the tree was previously infected and 0 otherwise); random block and plot effects were small and, therefore, omitted.

Western gall rust incidence during the 1990 and 1993 wave years was also predicted from annual height increment and previous infection status using model 1, with α = 0.15 (based on Wald's χ^2 test) used as a screening criterion for variable inclusion in (or exclusion from) both models. A generalised (Cox and Snell 1989) coefficient of determination (R^2; rescaled to maximum value 1) and area under the curve (AUC) were used to assess the ability of competing models to discriminate between infected and uninfected pine, where AUC = 0.5 for a model that performs no better than a random classification and AUC = 1 for a model that provides perfect discrimination of infected and uninfected trees.

To estimate volume reductions associated with stem infection (including indirect stem infection resulting from live branch galls being incorporated into stem tissue) by western gall rust, the following model (model 2) was fitted (as a first-order approximation):

$$\mathrm{VOL} = \beta_0 + \beta_1\mathrm{YTBH} + \beta_2\mathrm{HTINC_{BH}} + \beta_3\mathrm{DENS} + \beta_4\mathrm{ENCIRC} + \beta_5\mathrm{GHT} + \delta_{\mathrm{block}} + \gamma_{\mathrm{plot}} + \varepsilon_{\mathrm{tree}}$$

where VOL is the estimated gross volume (m^3) of an individual pine in 2011, YTBH is years for the subject pine to reach a height of 1.3 m, $\mathrm{HTINC_{BH}}$ is height increment (m) in the year in which the pine achieved 1.3 m, and DENS is the ($\log_{10}$) number of neighborhood trees of all species within 3.99 m (50 m^2) of the measured pine. For infected trees, ENCIRC is percent encirclement (10%) of the stem by the largest gall, as measured in 2011, and GHT is the corresponding height (m) of the largest gall. For uninfected trees, ENCIRC = 0 and GHT = 0. δ_{block}, γ_{plot}, and $\varepsilon_{\mathrm{tree}}$ are random errors, which were assumed to be mutually independent and identically distributed normal random variables, with mean 0 and respective variances $\sigma^2_{\mathrm{block}}$, σ^2_{plot}, and σ^2_{tree}. The predictors YTBH and $\mathrm{HTINC_{BH}}$ were included to adjust for individual-tree characteristics, treatment effects, and other factors that determine potential volume in the absence of infection (i.e., factors expressed before a tree attains breast height (1.3 m) — a period assumed to be free of

Table 1. Cumulative infection rates of lodgepole pine new tissue (stem, branch, and total) and old tissue (stem) by western gall rust in 2011 (year 24), cumulative stem infection by comandra blister rust in 2011, and cumulative branch infection by comandra blister rust in 1999 (year 12).

	Western gall rust				Comandra blister rust	
	New tissue			Old tissue		
Treatment	Stem	Branch	Total (stem or branch)	Stem	Stem	Branch
Coarse mixing	26.7±1.8	24.2±5.0a	37.1±2.9a	3.3	10.0±2.0	3.3±1.3
Trench–berm hinge	27.1±4.5	17.9±4.1ab	33.8±5.1a	0.4	9.6±3.3	4.6±2.1
Trench furrow	12.5±3.5	7.9±2.1b	17.5±4.4b	0.8	12.1±3.9	3.8±1.5
Burned windrow	24.6±5.4	21.3±3.6a	34.2±4.7a	2.5	12.1±2.2	3.8±1.5
Untreated control	19.2±2.7	15.8±2.3ab	29.6±2.9ab	2.5	6.7±1.8	2.1±1.3
p value	0.059	**0.033**	**0.020**	—	0.397	0.819

Note: The cumulative infection rate is the proportion of pine (live or dead) that had at least one infection in the indicated location. Values are mean percent ± 1 standard error; *p* values in bold indicate statistically significant treatment effects ($\alpha = 0.05$), and means with the same letter do not differ significantly according to the Bonferroni test. $n = 240$ trees·treatment^{-1}. Stem infection of new tissue by western gall rust includes both direct stem infections that originated on leader tissue and indirect stem infections resulting from live-branch galls being incorporated into stem tissue. Western gall rust branch infections are ≤10 cm from stem; comandra blister rust branch infections are ≤60 cm from the stem and were only recorded up to 1999. Old-tissue western gall rust infections were tallied separately from new-tissue infections and are in addition to the total reported for new tissue. ANOVA was not carried out on old-tissue infections due to the small sample size.

any measurable infection effects for the purpose of this analysis). The variable DENS was included to adjust for competition-related effects; plot-level (i.e., stand-level) density was examined but did not contribute significantly to the relationship. Only pine that were alive in 2011 and were either uninfected or had western gall rust stem infection (including indirect stem infection resulting from live-branch galls being incorporated into stem tissue) were included in the analysis; dead pine, comandra blister rust infected pine, and those pine with branch-only western gall rust infections were excluded. Gross volumes and losses (i.e., actual volume – potential volume = β_3ENCIRC + β_4GHT) were estimated for individual trees (cm^3·tree^{-1}) and then calculated for the stand level (m^3·ha^{-1}) by summing over trees and dividing by plot area. Treatment effects on individual-tree volume were assessed by performing an ANOVA (sources of variation are described above). All data analyses were performed using SAS statistical software (SAS Institute Inc. 2002–2010).

3. Results

3.1. Western gall rust infection

3.1.1. Cumulative infection and annual incidence

There were no significant differences in 24-year cumulative stem, branch, or total (stem and branch) infection rates of lodgepole pine by western gall rust between any of the site-preparation treatments and the untreated control ($P > 0.05$; Table 1). The trench furrow treatment, however, had significantly lower rates of branch and total infection than the coarse mixing and burned windrow treatments and also less total infection than the trench–berm hinge (Table 1; Fig. 1*a*). Considering the original population of 1200 pine at Bednesti, 30.4% had acquired at least one western gall rust stem or branch infection by age 24 years (Fig. 2*b*). For 8.4% of the total population, these were branch-only infections that died, leaving the tree uninfected by western gall rust in 2011. Of live stem infections in year 24, an average of 43% (range of 26%–53% across treatments) were indirect stem infections resulting from live-branch galls being incorporated into stem tissue (Table 2). In addition to cumulative stem infection rates (Table 1; Fig. 1*a*), an average of 1.9% (range of 0.4% to 3.3%; Table 1) of pine had western gall rust stem infections that originated on old (i.e., not current year) tissue, for which the infection year could not be determined. These galls were typically very small, appeared to be recently formed, and were clearly not present during earlier assessments.

Fig. 1. Cumulative rates of western gall rust stem infection of lodgepole pine (including indirect infections attributable to the incorporation of live branch galls into stem tissue). Infection rates (% of live and dead trees) are plotted for five site-preparation treatments: (*a*) by pine age (years) and (*b*) by mean height (cm) of all (infected or uninfected) trees alive at the end of each growing season between 1988 and 2011. Vertical markers indicate (*a*) the age and (*b*) the mean height when the last infection was recorded for each treatment.

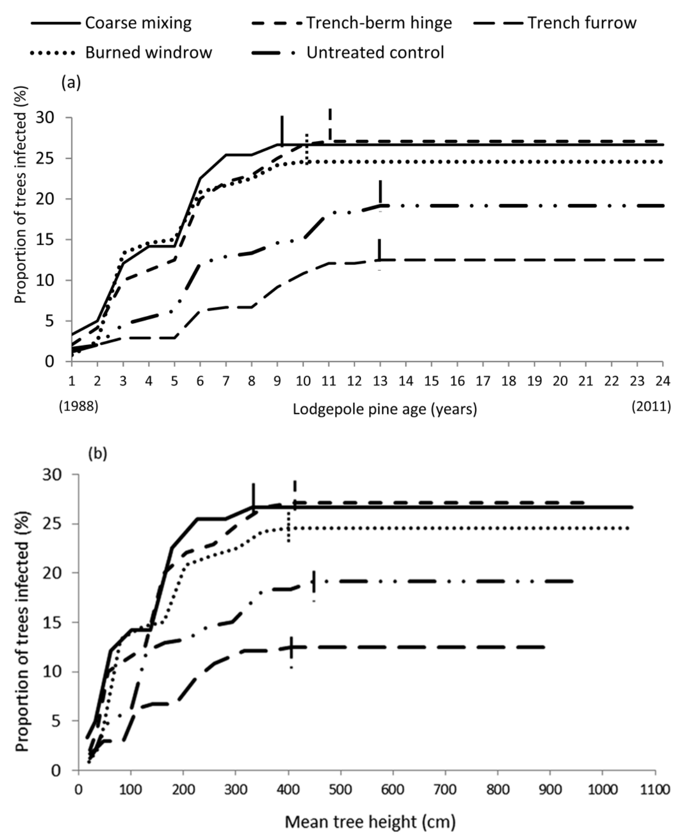


Fig. 2. (*a*) Proportion of lodgepole pine infected with western gall rust and (or) comandra blister rust as of 2011, (*b*) western gall rust infection location as of 2011, and (*c*) comandra blister rust infection location as of 2011. All percentages are the fraction of the total number of live and dead trees (*n* = 1200).

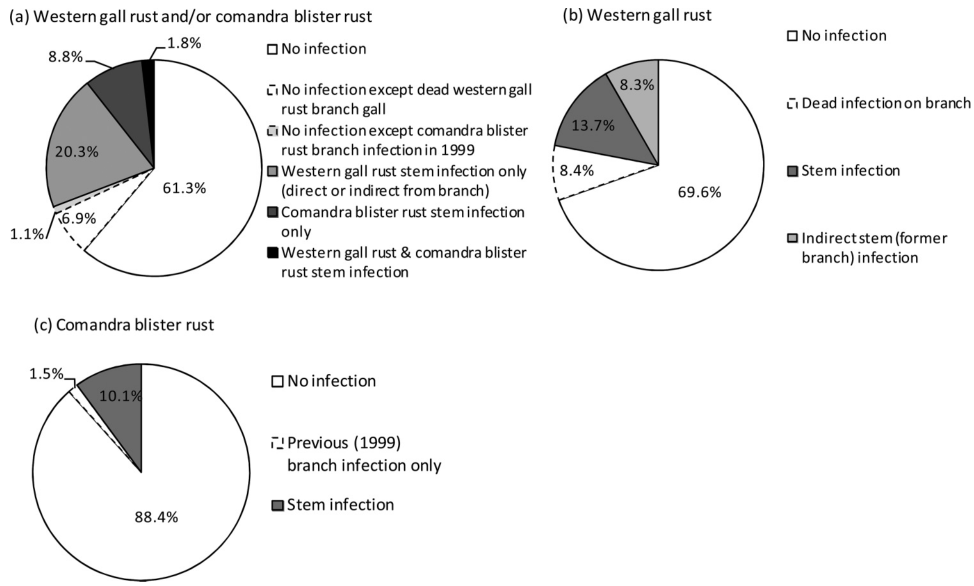
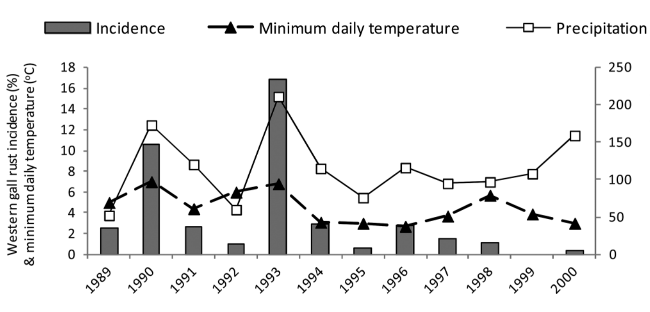


Table 2. Mean number of live-stem infections and stem-infection characteristics for western gall rust and comandra blister rust on live lodgepole pine in year 24 (2011).

	Western gall rust				Comandra blister rust		
Treatment	Infections per tree	Encirclement by largest infection (%)	Height of largest infection (cm)	Proportion of indirect stem infections (%)	Infections per tree	Encirclement by largest infection (%)	Height of largest infection (cm)
Coarse mixing	0.46±0.04a	42.3±2.4	103±11	45	0.06±0.02	73.7±9.5	29±3
Trench–berm hinge	0.42±0.06a	42.4±6.0	143±19	53	0.05±0.02	47.2±6.6	35 ±8
Trench furrow	0.16±0.05b	38.2±3.3	172±20	26	0.04±0.02	82.4±6.8	34±5
Burned windrow	0.48±0.11a	34.0±2.9	148±29	50	0.07±0.02	63.4±7.8	49±20
Untreated control	0.27±0.05ab	41.6±4.1	184±25	40	0.02±0.02	42.7±10.1	23±1
p value	**0.005**	0.477	0.137	—	0.224	0.161	0.910

Note: Values are mean ± 1 standard error except for the proportion of indirect stem infections, which is overall percentage for each treatment. Infections per tree means are calculated from the entire population of live pine (*n* = 1033) whether infected or not, whereas encirclement (%) and infection height (cm) means are calculated from the populations of pine infected by western gall rust (*n* = 257) or comandra blister rust (*n* = 43). *p* values in bold indicate statistically significant treatment effects (α = 0.05), and means with the same letter do not differ significantly according to the Bonferroni test. Indirect stem infection resulted from live-branch infections being incorporated into stem tissue. *p* values for heights of largest infections are based on ANOVA using $\log_{10}$ transformed data; however, untransformed means and standard errors are presented to facilitate interpretation. ANOVA was not done for proportion of indirect stem infections.

Fig. 3. 1989–2000 annual incidence (%) of western gall rust stem infection of lodgepole pine current-year leader tissue (regardless of whether the tree was previously infected) versus 15 May – 7 July total precipitation (mm; right *y* axis) and minimum daily temperature (°C; left *y* axis) at the Bednesti site.



The majority of infection by western gall rust occurred in the wave years 1990 and 1993 (Fig. 3), with the result that 74% of cumulative year 24 stem infection had occurred by the time that pine were 6 years old (1993) and 159 cm tall (Figs. 1*a* and 1*b*). The last western gall rust stem infections occurred in pine at ages 9, 10, and 11 years in the coarse mixing, trench–berm hinge, and burned windrow treatments, respectively, and at age 13 years in the trench furrow and untreated control treatments and corresponded with mean pine heights of 295, 413, 404, 413, and 455 cm in those years (Figs. 1*a* and 1*b*). The last western gall rust branch infection (within 10 cm of the stem) in any treatment was recorded in 1996 when pine were 9 years old, although the fact that small amounts of stem infection continued until 2000 suggests that small galls on new branch whorls 2–3 m above the ground may have been missed. By the time that pine were 24 years old, 64.1% of all branch galls (≤10 cm from the stem) recorded by 1996 were dead, and the remaining 35.9% were alive and had made contact with the stem, resulting in successful infection of stem cambial tissue. All stem galls recorded on live lodgepole pine in 2011 were live galls (Fig. 2*b*).

Significant correlations were found between the incidence of western gall rust and each of the individual climatic, pine characteristic, and site-preparation treatment variables tested, with the exception of mean annual pine height increment and the trench–berm hinge indicator (Table 3). None of the variables alone proved

Table 3. Logistic regression (model 1) analysis results predicting the incidence of western gall rust infection of current-year stem tissue (leader) during the period 1989–2000 from single factors related to climate, lodgepole pine host characteristics, or site-preparation treatment factors.

Factor type	Predictor	Unit	Maximum rescaled R^2 (%)	AUC	Likelihood ratio test prob ≥ χ^2
Climate	15 May–7 July precipitation	mm	13.3	0.76	<0.0001
	15 May–7 July minimum daily air temperature	°C	10.9	0.73	<0.0001
	15 May–7 July mean daily air temperature	°C	1.8	0.63	<0.0001
Lodgepole pine host characteristics	Age	year	4.7	0.67	<0.0001
	Height	cm	3.4	0.62	<0.0001
	Ground-level diameter	cm	2.6	0.60	<0.0001
	Previous western gall rust infection	1 vs 0	0.7	0.55	<0.0001
	Mean annual height increment	cm	0.1	0.51	0.176
Site-preparation treatment	Trench furrow	1 vs 0	1.2	0.56	<0.0001
	Coarse mixing	1 vs 0	0.3	0.53	0.0018
	Burned windrow	1 vs 0	0.3	0.53	0.002
	Trench–berm hinge	1 vs 0	0.1	0.52	0.105

Note: n is the total number of leader growth intervals; n = 13 590 for ground-level diameter and 13 616 for all other variables. Values used for pine age, height, and ground-level diameter are characteristics at the end of the growing season for the year in which extension of the leader occurred. For the period 1997–2000, when diameter was measured at DBH (1.3 m) rather than at ground level, ground-level diameter was estimated from DBH. Mean annual height increment is the mean from 1989 to the year of infection. Where the unit is "1 vs 0": for previous western gall rust infection, 1 indicates infected and 0 indicates uninfected; for site preparation treatments, 1 indicates the treatment was applied and 0 indicates no treatment (control). AUC, area under the curve.

to be a very powerful predictor of the incidence of western gall rust leader infection during the period 1989–2000. The best individual predictors were the climate variables, i.e., precipitation (maximum rescaled R^2 = 13.3%) and minimum daily air temperature (R^2 = 10.9%) (Table 3; Fig. 3); mean daily air temperature (R^2 = 1.8%) was the least effective predictor among the three climate variables tested. Variables relating to pine age, height, and diameter at the time of infection also proved to be relatively poor individual predictors of western gall rust infection, with R^2 values 4.7%, 3.4%, and 2.6%, respectively. Previous infection status and site-preparation treatment factors likewise appeared to have little individual predictive power with R^2 ≤ 1.6% and AUC ≤ 0.56. The "best" multifactor model (identified by stepwise selection of variables) for the period of 1989–2000 performed somewhat better (R^2 = 22% and AUC = 0.82; Table 4) than the single-factor models. Owing to the complexity of the infection process and obvious design limitations, the general lack of predictive power of the model is not surprising. Development of better models awaits further research.

For the 1990 and 1993 wave years, annual height increment and previous infection status resulted in an R^2 of 12%–13% for western gall rust incidence, with previous infection status making a stronger contribution to the models than annual height increment (Table 4). Parameter estimates for individual wave years were consistent with those covering the period 1989–2000 (cf. estimates for the three models in Table 4).

3.1.2. Infection intensity and characteristics

In 2011, the mean number of western gall rust stem infections on live 24-year-old pine (i.e., infection intensity) at Bednesti (n = 1033) did not differ between the untreated control and any of the other treatments but was significantly higher in the coarse mixing, trench–berm hinge, and burned windrow treatments than in the trench furrow (Table 2). There were no significant treatment effects on percent encirclement of pine stems by the largest gall or the height at which the largest gall occurred (p > 0.05; Table 2). On average, the largest gall encircled 39.7% of individual lodgepole pine stems. When the largest gall was grouped into 25% stem encirclement classes, 30%, 40%, 25%, and 5% of infections occurred in encirclement classes of ≤25%, 26%–50%, 51%–75%, and >75%, respectively. Largest galls occurred at a mean height of 150 cm, with the majority (81%) at or below 2 m (Fig. 1*b*). Of largest galls, the highest was recorded at 509 cm above the ground. We found a weak trend indicating that percent stem encirclement by the largest gall at pine age 24 years decreased with gall age (p = 0.050; R^2 = 4%).

3.2. Comandra blister rust infection

3.2.1. Cumulative infection

Site preparation did not significantly affect cumulative stem (to 2011) or branch (to 1999) infection of lodgepole pine by comandra blister rust (p > 0.05; Table 1), which averaged (for all treatments) 10.1% and 3.5%, respectively. Of the 139 pine (live or dead) that had comandra blister rust stem infections in 2011, 20 (1.7% of all pine) had branch-only comandra blister rust infections in 1999 (data not presented). An additional 18 pine with branch-only infections in 1999 (1.5% of all pine) did not develop stem infections by 2011 (Fig. 2*c*).

3.2.2. Infection intensity and characteristics

There were no site-preparation treatment effects on the number of comandra blister rust stem infections on live 24-year-old lodgepole pine (i.e., infection intensity), percent stem encirclement by the largest infection, or height above ground of the largest infection (Table 2). On average (including all infected and uninfected trees), pine at Bednesti had 0.05 comandra blister rust infections per tree. The largest comandra blister rust infections encircled an average 61.9% of the stem and occurred at a mean height of 25 cm.

3.3. Mortality and volume effects on lodgepole pine

3.3.1. Mortality due to western gall rust and comandra blister rust

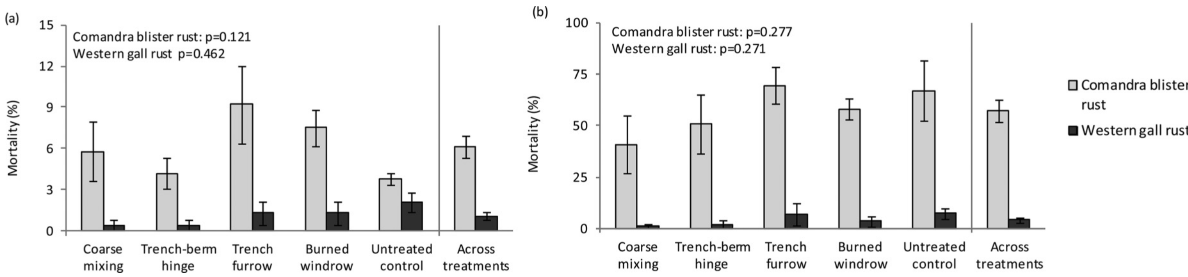
By the time that pine at Bednesti were 24 years old, averages of 1.1% and 6.1% of the total population of planted trees had died as a result of western gall rust or comandra blister rust infection, respectively. Site preparation did not significantly affect mortality caused by either of these rusts, regardless of whether the population in question was all pine or the subset of infected pine (p > 0.05; Figs. 4*a* and 4*b*). Of pine infected by western gall rust or comandra blister rust, an average 4.2% and 57.3%, respectively, had died by age 24 years.

Table 4. Estimated model 1 parameters for predicting incidence of western gall rust infection on current-year (leader) tissue for (*a*) 1989–2000 following a stepwise selection of factors (α = 0.15 for variable entry and (or) removal) and for (*b*) individual 1990 and 1993 wave years from height increment and previous infection status.

Period	Regression coefficient	Unit	Estimate	SE	Prob ≥ Wald χ^2	Maximum rescaled R^2 (%)	AUC	Likelihood ratio test prob ≥ χ^2
1989–2000	Intercept	—	−3.77	1.27	0.0029	22	0.82	<0.0001
	Pine height	cm	−0.0062	0.00229	0.0069			
	Mean annual height increment	cm	0.0687	0.0128	<0.0001			
	(Mean annual height increment)^2	cm^2	−0.00054	0.00016	0.0007			
	Pine age	year	−0.151	0.059	0.0101			
	Ground-level diameter	cm	0.169	0.076	0.0254			
	Previous western gall rust infection	1 vs 0	1.05	0.12	<0.0001			
	15 May–7 July precipitation	mm	0.0146	0.0018	<0.0001			
	15 May–7 July mean daily temperature	°C	−0.275	0.132	0.0368			
	15 May–7 July minimum daily temperature	°C	0.312	0.110	0.0045			
	Trench furrow	1 vs 0	−0.530	0.171	0.0019			
1990	Intercept		−4.49	0.52	<0.0001	13	0.73	<0.0001
	Mean height increment	cm	0.101	0.031	0.001			
	(Mean height increment)^2	cm^2	−0.00068	0.000044	0.12			
	Previous infection status	1 or 0	1.459	0.332	<0.0001			
1993	Intercept		−3.95	0.58	<0.0001	12	0.69	<0.0001
	Mean height increment	cm	0.106	0.032	0.001			
	(Mean height increment)^2	cm^2	−0.00123	0.000042	0.003			
	Previous infection status	1 or 0	1.460	0.181	<0.0001			

Note: For the period 1997–2000, when diameter was measured at DBH (1.3 m) rather than at ground level, ground-level diameter was estimated from DBH. Where the unit is "1 vs 0": for previous western gall rust infection, 1 indicates infected and 0 indicates uninfected; for site-preparation treatments, 1 indicates the treatment was applied and 0 indicates no treatment (control). SE, standard error; AUC, area under curve.

Fig. 4. Mortality (%) of 24-year-old lodgepole pine attributed to comandra blister rust and western gall rust for individual treatments and across all treatments expressed as (*a*) proportion of all pine and (*b*) proportion of pine infected with each disease.



3.3.2. Individual-tree and stand-level volume loss due to western gall rust and comandra blister rust

All variables in combination were found to be highly significant (|*t*| < 0.0001) predictors of individual-tree volume of western gall rust stem-infected pine (model 2), resulting in an overall R^2 of 54% (Table 5). Individual-tree volume-loss estimates among western gall rust stem-infected pine (relative to uninfected pine) did not differ significantly among site-preparation treatments regardless of whether they were examined as absolute losses (cm^3·tree^{-1}; p = 0.079) or as proportional losses (%·tree^{-1}; p = 0.268) (Table 6).

At the stand (plot) level, estimated uninfected-pine volume in individual treatments ranged from 45.4 to 78.9 m^3·ha^{-1}, estimated live western gall rust stem-infected volume ranged from 7.0 to 37.2 m^3·ha^{-1}, estimated live comandra blister rust infected volume (expected to die) ranged from 3.0 to 8.4 m^3·ha^{-1}, and estimated rust-related volume loss to mortality (comandra blister rust or western gall rust) and western gall rust related growth reductions among live pine ranged from 5.0 to 13.9 m^3·ha^{-1} (Fig. 5).

Table 5. Estimated model 2 parameters for predicting individual-tree volume (m^3·tree^{-1}) of live 24-year-old western gall rust stem-infected lodgepole pine (R^2 = 54%).

	Unit	Estimate	SE	Prob ≥ |*t*|
Intercept	—	0.1788	0.0077	<0.0001
Encirclement by largest gall	10%	−0.0031	0.0005	<0.0001
Height of largest gall	1 m	0.0053	0.0013	<0.0001
Years to reach breast height*	1 year	−0.0158	0.0008	<0.0001
Height increment at breast height*	1 m	0.0518	0.0067	<0.0001
Number of trees within 3.99 m ($\log_{10}$)*	1 tree	−0.0349	0.0047	<0.0001

Note: Predictors indicated by an asterisk (*) are included to adjust for (treatment related) differences in early growth and density of neighbourhood trees. SE, standard error; breast height, 1.3 m.

4. Discussion

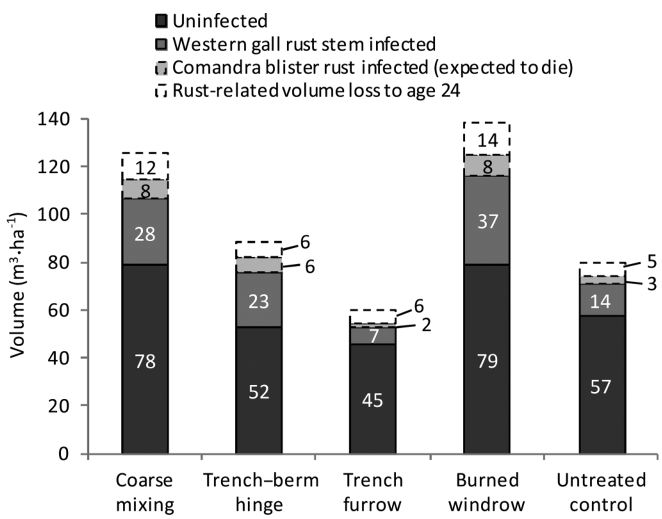
The site-preparation techniques tested at Bednesti did not significantly increase rates of lodgepole pine infection by western gall rust or comandra blister rust relative to the untreated control and neither did they result in significantly different infection characteristics. Although there were trends of increasing western gall rust infection rate and severity in treatments that stimulated the greatest pine growth response, they did not change the relative ranking of treatment-related growth gains relative to the control. We had anticipated this outcome; nevertheless, we wished to confirm that no treatment–rust interactions were occurring that could offset the long-term growth increases that were predicted

Table 6. Treatment effects on estimated (model 2) volume loss for individual western gall rust stem-infected lodgepole pine at age 24 years (2011).

		Volume loss	
Treatment	*n*	Absolute (cm³·tree⁻¹)	Proportional (%·tree⁻¹)
Coarse mixing	57	8525±1018	9.5±1.9
Trench–berm hinge	57	6144±1029	7.9±1.9
Trench furrow	26	4088±1372	9.0±2.5
Burned windrow	53	4643±1059	4.4±2.0
Untreated control	46	5558±1103	10.7±2.0
p value		0.079	0.268

Note: Values are mean ± 1 standard error. Population includes pine alive in 2011, excluding trees with comandra blister rust infection and trees with branch-only western gall rust infection.

Fig. 5. Age 24 years stand-level lodgepole pine uninfected volume, western gall rust stem-infected volume, comandra blister rust infected volume (expected to die), and volume already lost to rust effects (i.e., mortality caused by western gall rust or comandra blister rust plus growth losses in live western gall rust infected trees as estimated by model 2). Values in (or beside) bars represent volume (m³·ha⁻¹).



for some site-preparation treatments at this site (Cortini et al. 2010). Total infection levels were in agreement with other recent reports (Heineman et al. 2010; Woods 2011) and were higher than would have been anticipated when the stands were established in the 1980s (Nevill et al. 1996). Nonetheless, our study confirmed that the majority of infection took place prior to a stand age of 10 years. Finally, our estimates of rust-related volume losses, although admittedly crude, are the first such estimates for lodgepole pine stands in BC of which we are aware.

Although differences in western gall rust cumulative infection rates and infection severity did not differ significantly between individual site-preparation treatments and the untreated control, there were some significant differences between the trench furrow treatment, which tended to (nonsignificantly) reduce pine growth relative to the control (Boateng et al. 2012), and the coarse mixing, disk trenching, and burned windrow treatments, which improved pine growth. Other North American and European studies have similarly reported higher stem rust incidence among pine having the largest growth response to site-preparation (Desprez-Loustau and Wagner 1997) or thinning (van der Kamp et al. 1995) treatments — an effect that has been attributed to greater availability of susceptible host tissue.

In contrast to western gall rust, there were no observable trends suggesting that rapidly growing pine were more susceptible to comandra blister rust infection than slower growing trees. This contradicts earlier observations that comandra blister rust is more likely to infect vigorously growing pine (van der Kamp and Spence 1987). In theory, site preparation has the potential to increase rates of infection by comandra blister rust by stimulating the alternate host *Geocaulon lividum* (Richards.) Fern. to spread. This does not appear to have been an important factor at the Bednesti site, however, because there was no treatment effect on comandra blister rust cumulative infection rate. A related study also reported that the treatments at Bednesti did not stimulate large increases in the herbaceous plant community (Haeussler et al. 1999), which indirectly suggests little effect on *G. lividum*.

By the time that the Bednesti stand was 24 years old, 31% of all planted lodgepole pine had sustained at least one western gall rust or comandra blister rust stem infection, which is similar to or higher than infection rates reported in other recent studies from central interior BC (Heineman et al. 2010; Woods 2011). For western gall rust, the early high rates of infection at Bednesti are likely related to the occurrence of two wave years (1990 and 1993) by the time that the stand was 6 years old. Western gall rust wave years occur when cool, humid conditions in early summer coincide with spore release and the availability of susceptible host tissue (Peterson 1971) and have historically been observed to occur about once a decade (van der Kamp 1994). Unpublished data collected in relatively close proximity to the Bednesti site suggests a higher frequency in this particular geographic area, with as many as eight wave years observed between 1988 and 2011 (R. Reich, unpublished data). At Bednesti, early summer (15 May – 7 July) precipitation was the best individual predictor of annual incidence of western gall rust among the factors that we examined, with minimum daily temperature a close second. High humidity and constant moderate temperature are optimal conditions for infection by western gall rust (Adams 1997), and Fig. 3 clearly illustrates the peaks in seasonal precipitation and daily minimum temperature that coincided with high incidence of western gall rust during the 1990 and 1993 wave years.

The majority of western gall rust infection is believed to take place before age 10 years (Blenis and Li 2005) and at heights <2 m (van der Kamp 1994). On the whole, the Bednesti results were consistent with these assumptions, although minor amounts of stem infection did continue to age 13 years and heights of 509 cm. On 1.9% of lodgepole pine at Bednesti, we also observed small infections that appear to have originated on older tissue, usually at the site of small wounds. Although this contradicts the widely accepted belief that western gall rust infection is restricted to current-year tissue (Hopkin et al. 1988), we hypothesize that breaks in the bark may have rendered the inner tissue susceptible to infection. This proposition seems reasonable in view of research showing that lodgepole pine susceptibility to western gall rust declines with the degree of leader elongation (and by association with the degree of suberization of leader tissue) (Moltzan et al. 2001). Although it is possible that these small galls are latent infections, histology observed in cross sections from similar galls in companion studies does not fit with that model. Further research is required to investigate this phenomenon, as it has been observed elsewhere (R. Reich, unpublished data) and implies that low levels of infection by western gall rust may continue for many years.

There is disagreement in the literature as to whether susceptibility to western gall rust is governed primarily by age of the pine host (Blenis and Li 2005) or by host height and its relationship to the proportion of susceptible tissue and microclimatic conditions in the canopy (van der Kamp et al. 1995). We can contribute little to the debate — both factors were significant in a multiple regression model for predicting annual incidence of western gall rust, with height making the slightly stronger contribution. A complex web of temporally and spatially variable factors is obviously involved in the process of host tissue infection; however, our experiment is limited to a relatively narrow range of conditions at one site and was not specifically designed to investigate causal factors in a controlled manner.

Comandra blister rust generally has lower incidence than western gall rust in BC, but it is considered to be the more serious pathogen, because in our region, it nearly always kills its lodgepole pine host by age 30 years (Hiratsuka et al. 1988). The lethality of comandra blister rust in BC contrasts with its effects further south in North America, where it may exist on mature trees without killing them (Geils and Jacobi 1993). At Bednesti, our finding that nearly 60% of comandra blister rust infected pine were dead by age 24 years and that surviving infected trees had an average 62% stem encirclement is consistent with this belief. There is some uncertainty as to whether or not comandra blister rust branch infections are lethal (van der Kamp 1988; Hiratsuka et al. 1988). Our study, in which slightly more than half of the pine that had comandra blister rust branch infections at age 12 years (1999) subsequently developed stem infections by age 24 years, suggests that pine trees with comandra blister rust infected branches are at increased risk of mortality relative to uninfected trees.

Western gall rust infection, on the other hand, did not result in rapid death of lodgepole pine at Bednesti. Others have also noted that stem galls may be present for many years (Allen et al. 1996) or until stem encirclement exceeds 79%–90% (Wolken et al. 2006) without killing the host tree. Only 4.2% of western gall rust stem-infected pine had died by age 24 years in our study, and 30% of live infected trees had ≤25% stem encirclement. Therefore, it is reasonable to assume that at least some of these infected pine will persist to rotation age, particularly if stands are harvested as early as age 50–60 years as managers struggle to address midterm timber supply shortfalls resulting from the mountain pine beetle epidemic (BC Ministry of Forests, Lands and Natural Resource Operations 2011). Although unanticipated mortality losses are considered the most important factor governing the productivity of managed stands (Flewelling and Monserud 2002), quantifying growth losses among live western gall rust infected pine is also important for the accurate prediction of stand yield.

Western gall rust infection is assumed to cause growth losses among lodgepole pine, but these have not been well quantified. Infection reduces the ability of lodgepole pine to conduct water without affecting whole-tree water relations (Wolken et al. 2009), which suggests that the tree compensates for the former effect by reducing growth. Therefore, stem encirclement by the largest gall was expected to be a good predictor of volume loss, and we identified (by adjusting for other tree and density factors) a significant positive relationship between percent stem encirclement and individual-tree volume loss. Volume loss also increased inversely to height of the infection. On average, individual, live infected pine had 8.3% less volume than uninfected pine, which is similar in magnitude to individual-tree volume loss reported for lodgepole pine in a central US study that were infected, but not girdled, by comandra blister rust (Geils and Jacobi 1993). In our study, percent stem encirclement by western gall rust was highly variable within individual site-preparation treatments, and there were no significant treatment effects on either absolute ($cm^3 \cdot tree^{-1}$) or proportional ($\% \cdot tree^{-1}$) individual-stem volume loss. We were unable to identify any trends to explain the wide variation in percent stem encirclement at Bednesti, which ranged from 5% to 93% even among the population of galls that originated in the same (1993) wave year. Likewise, Blenis and Duncan (1997) found no relationship between percent stem encirclement and either gall age or gall height.

Woods and Coates (2013) emphasize the importance of taking into account the ongoing effects of damaging agents on stand development. Our results confirm that mortality caused by hard pine stem rusts, mainly comandra blister rust, accounted for the majority (about four-fifths) of lodgepole pine volume loss to age 24 years. Nonetheless, growth losses among live western gall rust infected trees were also large enough (about one-fifth of total estimated volume loss) to warrant consideration. Across all site-preparation treatments at the 24-year-old Bednesti site, we estimated that current total stand-level volume loss to rust-related mortality and growth reductions among live western gall rust infected trees was 8.4%.

5. Management implications and conclusions

Our primary study objective was to examine interactions between site-preparation treatments applied at Bednesti and the rate and intensity of western gall rust or comandra blister rust infection. We wanted to consider the implications with regard to both early stand management decisions and longer term growth and yield predictions. In particular, it was important to determine whether treatment-related differences in rust presence were likely to reduce or negate lodgepole pine growth responses that had been projected over the course of a rotation (Cortini et al. 2010). We conclude that, in spite of the fact that there will be losses resulting from hard pine stem rusts, they are unlikely to impact the relative long-term gains achieved by site preparation. Although there were trends of higher estimated individual-tree and stand-level volume losses in the treatments that produced the largest growth responses (coarse mixing and burned windrow) (Boateng et al. 2012), the volume losses did not change the relative ranking of lodgepole pine growth response to treatment (Fig. 5).

From the perspective of juvenile lodgepole pine management, the Bednesti study supports the assumption that the majority of infection by both western gall rust and comandra blister rust occurs within the first 10 years. However, this is not an absolute principle, and further minor infection by western gall rust should be anticipated. Although our results generally support the conclusion that hard pine stem rust presence is stable at the time that stands are returned to government responsibility at age 10–15 years, they do not support any reductions in the age at which this transfer occurs. Furthermore, anticipated rates of infection and expected mortality must be taken into account, perhaps in the form of adjustment to prescribed planting densities.

The significance of western gall rust branch infection is important to the establishment of criteria for acceptable stand condition prior to responsibility being returned to the government. The Bednesti study suggests that western gall rust branch infections occurring within 10 cm of the stem are much less likely to impact pine condition than stem infections; approximately two-thirds of these branch galls died before they made contact with stem tissue. The remainder became indirect stem infections that were incorporated into stem tissue at the hinge of the branch and stem. In 2011, these indirect infections comprised 43% of the western gall rust stem infections that were present on live pine. They appear to be less serious than infections that originated on leader tissue, because they penetrate less deeply into the bole and are probably less likely to result in stem breakage. It is anticipated that future assessment of hard pine stem rust status at the Bednesti site will increase our understanding of the progression of these diseases and their effects on stand development and projected volume at rotation. In particular, further investigation is required regarding the relationship between density, crown lift, and branch gall longevity.

Although a generalized estimate of volume loss to damaging agents is applied in timber supply planning in BC, volume-loss information specific to most individual pathogens and insects, including western gall rust and comandra blister rust, has not been available for incorporation into the modeling process (Woods et al. 2010). Our approach to estimating volume loss at Bednesti was necessarily a first approximation due to limitations imposed by the experimental design (i.e., because the study was not specifically designed to investigate the effects of rust disease, we had limited ability to adjust for confounding factors), the relatively small sample size, and the obvious inadequacies in our (linear) tree- and stand-level (i.e., plot-level) models, which do not, for example, consider the long-term and large-scale spatial effects of mortality and infection on the subsequent growth of neighbouring trees. Nonetheless, our results suggest that western gall rust related growth losses are large enough that they should be considered along with mortality in future modeling exercises. Moreover, the Bednesti data are potentially useful for designing future studies and might be used to incorporate at least some of the effects of hard pine stem rusts into more sophisticated growth and yield models that simulate the interplay of stand-level dynamics (e.g., gap creation due to mortality) and individual-tree growth. For example, TASS (tree and stand simulator; Mitchell 1975), which is currently used to model timber supply in BC, has already been adapted to include the effects of certain other pathogens and insects.

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