

Long-Term Effects of Lodgepole Pine Terminal Weevil and Other Pests on Tree Form and Stand Structure in a Young Lodgepole Pine Stand in Southern British Columbia

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Abstract

This study describes the impacts of 25 damaging agents recorded on young lodgepole pine trees over a 30-year period in a study plot in southern British Columbia. During the study, density fluctuated due to infill and mortality. Of the 1,295 stems per hectare present at the outset of the study, 37% of lodgepole pine died and only 24% of the trees remained pest-free by the final assessment. Pest-free trees were predominantly small and suppressed infill, leaving just over 1,000 stems per hectare of crop trees. Lodgepole pine terminal weevil affected over 38% of pine, with up to six attacks per tree. Fifty percent of lodgepole pine in the study was infected or killed by one or more hard pine stem rusts, with comandra blister rust and western gall rust being the predominant diseases, affecting 32% and 19% of the pine, respectively. Until age 20, 70% of weevil attacks caused major defects. From age 20–40 years, 50% of attacks caused major defects, often forks or multiple tops (stag-heads). Defects were more severe when trees were attacked early in stand development. There was a strong correlation between the number of weevil attacks per tree and tree form, and the number of pests recorded per tree and tree form. Two or more pests per tree caused tree form to shift from good to moderate or poor.

KEYWORDS: young lodgepole pine; damaging agents; monitoring; forest health; tree form

Introduction

Changing climate, pest activity and, fire affect the health, productivity, and economic expectations of regenerating forests across a wide range of forested ecosystems in British Columbia (Woods et al. 2010, Sturrock et al. 2011, Maclauchlan et al. 2015, Woods et al. 2017, FLNRORD 2019, Maclauchlan & Buxton 2019, Maclauchlan 2020). Lodgepole pine, *Pinus contorta* Dougl. ssp. *latifolia* (Engelm.), is the dominant species in most dry, cold forests of western North America, forming pure successional stands or co-dominant mixtures (Klinka et al. 2000). The forests of British Columbia cover an area of just over 60 million hectares (Government of British Columbia n.d.) and lodgepole pine is the most ubiquitous tree species found throughout the interior of the province. Numerous pests affect lodgepole pine throughout its rotation, with the dominant natural disturbance agents

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of mature lodgepole pine being the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Curculionidae; Scolytinae) (Safranyik & Carroll 2006, Amoroso et al. 2013, Westfall & Ebata 2017, Negron & Cain 2019) and stand replacing fires (Lotan et al. 1985, Klutsch et al. 2011, Kulakowski et al. 2012). Mountain pine beetle (MPB) populations periodically erupt, killing thousands of hectares of mature or nearly mature pine trees (Safranyik & Carroll 2006, Alfaro et al. 2015, Maclauchlan et al. 2015, Walton 2016, Axelson et al. 2018). At least four large-scale outbreaks of mountain pine beetle have occurred in western Canada in the past 120 years, either documented in forest survey records or detected as growth releases in tree rings (Alfaro et al. 2004, Taylor et al. 2006, Axelson et al. 2010, Westfall & Ebata 2017, Axelson et al. 2018). Alfaro et al. (2004) identified three large outbreaks through tree ring analysis: 1890s, 1940s, and 1980s, with many smaller, more localised outbreaks occurring between these major events. The most recent MPB outbreak in British Columbia began in the late 1990s, peaking in 2007 at over 10 million hectares affected (Walton 2016, Westfall & Ebata 2017). By 2008, the beetle had affected almost 14 million hectares of pine forests, an area 10 times larger than in any previously recorded outbreak (Safranyik et al. 2010). Since that time, the area affected has declined rapidly to pre-outbreak levels with only 119,089 hectares affected in 2017 (Westfall & Ebata 2018).

In addition to extensive mature timber loss, MPB epidemics may increase fuel loading, leading to more severe wildfires and altering successional trajectories and a myriad of other resource values (Safranyik et al. 1974, McGregor 1985). Gray (2013) found that the hazard and risk of wildfire increased as the dead overstory of unsalvaged, MPB-impacted stands decayed and fell. Many of the stands that burned in British Columbia's 2017 and 2018 massive wildfires were killed by MPB over a decade ago and were on the ground when the fires struck, creating massive amounts of fuel.

These cumulative disturbances on the land base of British Columbia have dramatically accelerated harvesting and reforestation efforts. In addition to the extensive new plantations resulting from MPB harvest, British Columbia is now challenged with reforesting extensive areas that were burned in the 2017–2018 wildfires (Fletcher 2018). The result will be a vast landscape of young forests, many composed of pure lodgepole pine or mixtures of lodgepole pine and other species.

Despite the vast area of young stands in the interior of British Columbia, there is a paucity of published data on the incidence, severity, and impact of pests affecting regeneration (Bella 1985, Alfaro 1989, Maclauchlan & Borden 1996, Heineman et al. 2010). Bella (1985) warned that by significantly reducing stand density, young lodgepole pine stands could be at risk to growth loss, reduction in quality, and even mortality from various damaging agents. One of the most common insect pests of lodgepole pine is the lodgepole pine terminal weevil, *Pissodes terminalis* Hopping (Drouin et al. 1963, Retnakaran & Harris 1995, Maclauchlan & Borden 1996, Heineman et al. 2010). The lodgepole pine terminal weevil has been recorded attacking lodgepole pine in Yukon Territory, BC (Drouin et al. 1963, Maher 1981, Heineman et al. 2010), east into Saskatchewan and Manitoba (Hopping 1920, Drouin et al. 1963, Bella 1985, Retnakaran & Harris 1995), and south through California (Cameron & Stark 1989). Most studies of this insect look at host selection, biology, and attack dynamics (Maher 1981, Cameron & Stark 1989, Maclauchlan & Borden 1996). However, there is little information on the long-term damage caused to the host due to lodgepole pine terminal weevil attacks. Whereas, the effects of attack by the Sitka spruce weevil, *Pissodes strobi* (Peck.) on Sitka spruce, *Picea sitchensis* (Bong.) Carr, and Norway spruce, *Picea abies* [L.] Karst., are well described (Alfaro 1989, Alfaro & Omule 1990, Daoust & Mottet 2006).

In addition to terminal weevil, there are numerous insect, disease, animal, and abiotic pests that affect young lodgepole pine stands in the southern interior of British Columbia. Notable pests of young pine include: western gall rust (*Cronartium harknessii* [J.P. Moore]) (Aime et al. 2018); comandra blister rust (*Cronartium comandrae* Peck); stalactiform blister rust (*Cronartium coleosporioides* Art.) (Powell & Hiratsuka 1973, van der Kamp & Spence 1987, van der Kamp 1994); and foliar diseases such as *Lophodermella concolor* (Dearn) and *Elytroderma deformans* (Weir) (Allen et al. 1996). Young pine is also affected by damaging agents that attack below-ground or at the lower bole, such as Armillaria root disease (*Armillaria ostoyae* [Romagnesi] Herink) (Cleary et al. 2008), Warren's root collar weevil (*Hylobius warreni* Wood) (Alfaro & Fuentealba 2016), and the Yosemite bark weevil (*Pissodes schwarzi* Hopk.) (Wood 1964). Damage by squirrels, hares (Sullivan & Sullivan 1982), bears (Sullivan 1993), and occasionally other mammals can kill trees or affect the growth and form of young pine in the southern interior. These afflictions, in combination with changing climate (e.g., drought) and the defects produced from terminal weevil attack may have serious repercussions on pine regeneration and future timber suitability.

The lodgepole pine terminal weevil attacks and kills the expanding terminal growth (leader) of young pines, causing minimal diameter loss but possibly affecting height and quality of attacked trees. Lateral branches below the killed leader assume dominance and a defect may form at this location on the tree bole. This insect has an extremely flexible life history (Cameron & Stark 1989, Kovaks & McLean 1990) dependent upon weather, and causes a range of growth defects, dependent upon ecosystem, tree age and size, and stand density (Stark & Wood 1964, Stevenson & Petty 1968, Stevens & Knopf 1974, Maher 1981, Maclauchlan & Borden 1996). From late June through July, female weevils select the largest terminal leaders in a stand where they feed, mate, and oviposit in the new terminal growth. One female weevil may oviposit in, and kill, many leaders. Early instar larvae feed circumferentially in the phloem of the new leader, effectively girdling and killing the new growth. Larvae then move to the pith and complete development. Dependent upon ecosystem and annual weather conditions, larvae will overwinter and emerge the following summer. In warmer sites, new adults may emerge in late summer to overwinter in the duff.

Between 1985 and 1991, 17 fixed area plots were established throughout the southern interior of British Columbia to study the incidence and impact of lodgepole pine terminal weevil and other damaging agents in regenerating lodgepole pine stands. This study looks at individual trees in one of the 17 plots in the south Okanagan over three decades, to describe and analyse the cumulative effect of the lodgepole pine terminal weevil and other damaging agents on tree development over time. This in-depth analysis of the effect of pests over time lays the foundation for future analysis of all plots in this study. This article's hypothesis is that trees affected by fewer pests over time will have better form. Insight into the challenges facing these new plantations as they develop may assist in future reforestation, stand management decisions, and provide valuable data for Timber Supply Analysis.

Methods

This study records the attacks by the lodgepole pine terminal weevil and other damaging agents on individual trees in a young lodgepole pine stand regenerated after the 1970s MPB outbreak. In 1985, a 0.22-hectare plot was established 18 km east of Okanagan Falls, BC. (49°18'19.57"N; 119°23'7.60"W) (elevation = 1,460 m) on Tree Farm License (TFL 59, formerly TFL 15). The plot lies on the transition of the Interior Douglas-fir dry, mild variant 1 (IDFdm1) (biogeoclimatic zone, subzone, and variant) and Montane Spruce dry, mild

variant 1 (MSdm1) (Lloyd et al. 1990, Meidinger & Pojar 1991). Originally, the site was a mature lodgepole pine stand that was killed by mountain pine beetle and subsequently logged in 1974. Portions of the stand were planted (1,200 stems per hectare) and others were left to regenerate naturally. In 1984, when the average tree age was eight years, the stand was operationally spaced to a 3-metre inter-tree distance (approximately 1,295 stems per hectare). At plot establishment, 285 trees were permanently tagged, stem mapped (Maclauchlan & Borden 1996), measured, and assessed for insect, disease, and other damaging agents.

The Okanagan Falls plot was assessed seven times over a period of 30 years (1987, 1993, 1996, 1999, 2010, 2014, and 2017) and assessments of tree growth, mortality, pest incidence, and tree impacts are described. In 1996 and 1999, additional trees within the plot boundary (infill trees greater than 1.3 m height) were tagged with unique tree numbers and added to the plot total. All above- and below-ground pest occurrence and damage from biotic and abiotic agents such as lodgepole pine terminal weevil, comandra blister rust, western gall rust, Armillaria root disease, suppression, and animal damage were recorded (BC MOF 2001, BC MSRM 2005) at each assessment time. Measurements and observations recorded in most assessment years included height (cm); diameter at breast height (DBH) (cm); year of lodgepole pine terminal weevil attack; height to each new weevil attack (measured from the base of the affected leader); and defect caused by weevil attack. In some assessment years, outbreaks of a needle disease (e.g., *Lophodermella*) affected most trees in the plot, and then, a general comment regarding stand infection for that assessment year was made.

Over time, as trees grew taller and crowns became more developed, determining the year of weevil attack was difficult. With each assessment, all past attacks were evaluated and a defect category for that assessment year was assigned. The defect might have remained unchanged or have increased or decreased in severity with tree development.

To more fully describe the effect of damaging agents on tree development, we defined three tree form categories, which were based on ocular estimates of general stem form (presence/absence of defects on main stem) and branch characteristics (thick, branchy trees vs. smaller diameter branches that self-prune). The three tree form categories are:

1. Good: straight stems with minimal pest damage, having no noticeable stem defects; branches are self-pruning and small;
2. Moderate: minor stem defects or pest damage; trees are branchy and there may be stem wounds; and
3. Poor: major stem defects and pest damage; poor stem form and trees are typically very branchy.

We then tested our hypothesis that trees with better form would have fewer recorded pests by comparing our ocular estimate of tree form to the incidence of pests recorded on each tree.

Four categories of stem defect were used to describe lodgepole pine terminal weevil attack (Maher 1981, Alfaro 1989, Maclauchlan & Borden 1996):

1. Crease: linear indentation, but little or no stem curvature at point of attack (minor, no impact);
2. Crook: major defect, occurring when a lateral assuming dominance is offset from the main stem by at least half the stem diameter;
3. Fork: major defect occurring when two laterals assume dominance (of equal or near equal length); and
4. Staghead: three or more laterals of equal dominance.

Summary statistics were compiled for all trees in the plot at each assessment time, including

- Damaging agents observed and year affected;
- Percentage of trees and stems per hectare affected by damaging agents;
- Number of live and dead lodgepole pine and other species;
- Average DBH (cm) of live and dead lodgepole pine;
- Average height (cm) of live trees;
- Tree form (1 = good, 2 = moderate, 3 = poor); and
- Average branch diameter (cm) at final assessment.

For some analyses, trees were assigned to a silviculture layer (BC MOF 1992) based on DBH and height to illustrate stand development over time:

Layer 1 = mature layer (≥ 12.5 cm DBH and over 1.3 m height);

Layer 2 = pole layer (7.5 to 12.49 cm DBH and over 1.3 m height);

Layer 3 = sapling layer (0 to 7.49 cm and over 1.3 m height); and

Layer 4 = regeneration (less than 1.3 m height).

Foresters managing TFL 59 (Weyerhaeuser Okanagan Falls Division, pers. comm.) developed their own evaluation of tree quality (or form) by measuring the diameter of branches present on trees at DBH (1.3 m height). The authors conducted a similar evaluation in 2016 to complement their evaluation. The number of live and dead branches at 1.3 m height on each tree was recorded and the diameter (2 cm from main bole) of a representative live branch was measured. The average number and diameter of branches in each form category was compared by analysis of variance and post-hoc Tukey HSD multiple comparison.

The DBH of live lodgepole pine and dead lodgepole pine were compared (*t*-test, $P < 0.05$) in each of the five assessment years (1996, 1999, 2010, 2014, 2017) that DBH was measured. When a tree died, the causal agent was determined; however, height and DBH were not recorded. For dead trees, the DBH of the last assessment was used for comparison. The authors also determined the DBH of trees infected and killed by comandra blister rust. Because assessments were not done every year, the DBH taken at the last assessment when the tree was still alive was used for this calculation.

The authors compiled frequency tables to examine the total number of pests recorded on each tree compared with tree form. The total number of pests (continuous variable) was compared with tree form (categorical variable) using a polyserial correlation (Chi square analysis) (SAS 2004). The authors also analysed the presence of animal damage and compared with tree form. Squirrel and hare are known to cause severe damage to trees; therefore, a variable was created where 0 = no squirrel or hare recorded and 1 = either or both mammals were recorded.

The percentages of lodgepole pine in 1996 and 2014 affected by lodgepole pine terminal weevil, comandra blister rust, stalactiform blister rust, and western gall rust were compared between years (*t*-test; $P < 0.05$). The frequency of live pest-free lodgepole pine and those affected by pests was also compared in these two assessment years (1996 and 2014) (Chi square analysis, $P < 0.05$).

A Pearson's Chi-square test was performed on the number of years from initial attack by the lodgepole pine terminal weevil and the final defect recorded (all trees, at all years), thus allowing the inclusion of trees that might have died prior to the final assessment in 2017. A Pearson's Chi-square test was also performed on the final defect code in 2017 vs.

the years since attack. The severity of defects observed in the final 2017 assessment was compared to the time elapsed (number of years) from when the weevil attack occurred. If trees died, the last defect assigned before death was used.

A correlation analysis was conducted of the total number of weevil attacks per tree over time vs. final tree form (Chi square analysis, $P < 0.05$).

Results

At establishment of the Okanagan Falls 0.22-hectare plot in 1985, there were 285 live lodgepole pine, or 1,295 stems per hectare (sph) (Table 1) and no other species measuring 1.3 m or higher. In 1987, the average DBH and height (\pm standard error) was 4.0 ± 0.1 cm and 280.6 ± 6.5 cm, respectively. In 1999, live lodgepole pine infill trees were small with an average DBH of 2.0 ± 0.1 cm (\pm standard error) compared to live lodgepole pine main-plot trees with an average DBH of 12.0 ± 0.2 cm. By 2014, live lodgepole pine infill trees had an average DBH of 2.9 ± 0.2 cm and live lodgepole pine main-plot trees had an average DBH of 16.6 ± 0.3 cm. Infill was suppressed and suffered high mortality from competition and pests, primarily comandra blister rust and western gall rust. Some infill was missed in later assessments because the trees had fallen, decayed, or been covered by vegetation. There were only 15 trees of other species in the plot, all of which were infill: three western larch, *Larix occidentalis* Nutt.; and, 12 interior spruce, *Picea glauca* (Moench) Voss subsp. *engelmannii* (Parry ex Engelm.) hybrids. The number of live pines in the plot fluctuated over the 30 years of monitoring with the final count in 2017 being 371 live (1,686 sph) and 219 dead (995 sph). By 2017, the DBH of live pine and dead pine averaged 13.1 ± 0.4 cm and 5.7 ± 1.2 cm (\pm SE), respectively (Table 1) and the height of live pine averaged just less than 10 m. The mean DBH of live pine was significantly larger than that of dead pines (Table 1), once the trees began to grow and differentiate structurally, beginning in 1999 and continuing through 2017.

Table 1. Density (stems per hectare) of live and dead lodgepole pine and other species in the Okanagan Falls plot at seven assessment times (1987–2017). The average diameter at breast height (DBH) (\pm SE) of all live and dead lodgepole pine and height (\pm SE) of live pine (three measurement years) are shown. DBH of live and dead trees are compared using the DBH of the measurement year prior to death.

Year	Density (sph) lodgepole pine (PI) ¹		Other spp. (live)	Avg. DBH (\pm SE) (cm) ²		Height (\pm SE) (cm)
	Live	Dead		Live PI	Dead PI	
1987	1,295	0	0	4.0 ± 0.1		280.6 ± 6.5
1993	1,100	91	0	8.7 ± 0.2		
1996	2,045	118	45	6.6 ± 0.2	6.8 ± 1.8	506.3 ± 12.3
1999	2,468	250	64	7.6 ± 0.3	$4.1 \pm 0.8^*$	
2010	2,027	773	68	10.4 ± 0.4	$3.4 \pm 0.3^*$	
2014	1,850	964	59	12.2 ± 0.4	$4.0 \pm 0.5^*$	995.7 ± 21.3
2017	1,686	995	50	13.1 ± 0.4	$5.7 \pm 1.2^*$	

1. Ingress were tagged and added to plot in 1996 and 1999

2. DBH of live and dead PI followed by an * are significantly different (t -test; $P < 0.05$) dbh, diameter at breast height; SE, standard error; sph, stems per hectare; spp, species.

Figure 1 illustrates how stand structure has changed over time, with the majority of lodgepole pine falling within Layer 3 in 1987. By 2014, most of the original plot trees had become Layer 1, with some Layer 2 and 3 trees. Layer 3 trees were infill and suppressed, and most Layer 2 trees were also infill and unlikely to become crop trees.

Up to seven different pests were recorded on individual lodgepole pine trees. In total, five types of wildlife damage, seven diseases (including two needle diseases, three stem diseases, one stem canker, and lodgepole pine dwarf mistletoe), seven types of insect damage, and six categories of miscellaneous (abiotic) damage were recorded affecting lodgepole pine (Table 2). Although moose feeding was the most common animal damage recorded, the damage usually occurred on suppressed or infill trees and impact was not severe. Hares, squirrels, and porcupines caused the most severe feeding damage, affecting over 12% of trees in the plot. Squirrel feeding is often found on trees infected with stem rusts, such as comandra blister rust and western gall rust (Burleigh et al. 2014). There were two outbreaks of *Lophodermella* needle disease during the 30-year monitoring period, lightly affecting most trees in the plot, but with little to no visible damage other than minor foliage loss. The most prevalent and damaging diseases were comandra blister rust and western gall rust that affected about 32% and 19% of the pine, respectively (Table 2). Both diseases can cause mortality and/or stem deformity. Stalactiform blister rust, also a mortality agent, was present at a much lower level, affecting 5% of pine. The lodgepole pine terminal weevil affected more trees than any other single damaging agent did. Of the 407 live pines in 2014, over 38% were attacked one or more times by this weevil. Mountain pine beetle killed less than 1% of the pine and all other insects recorded in the plot occurred at low levels and caused little or no damage to host trees (Table 2).

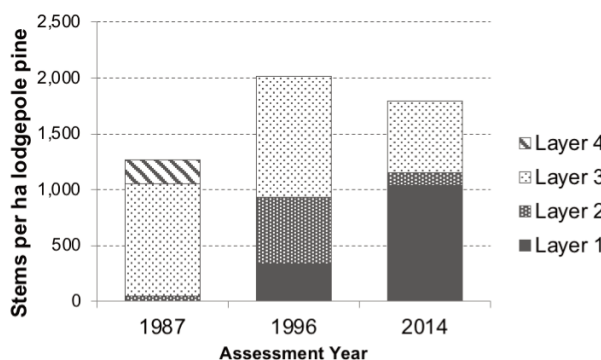


Figure 1. Density (stems per hectare) of lodgepole pine (original plot trees plus infill) by silviculture layer in three assessment years. Layer 1 = mature layer (> 12.5 cm DBH and > 1.3 m height); Layer 2 = pole layer (7.5 cm to 12.49 cm DBH and > 1.3 m height); Layer 3 = sapling layer (0 to 7.49 cm and > 1.3 m height); Layer 4 = regeneration (height less than 1.3 m) (BC MOF 1992).

Table 2. Cumulative list of damaging agents affecting lodgepole pine in the Okanagan Falls plot (1987–2014) (percentage of trees affected and still alive in 2014).

Damaging agents	Percentage of trees affected
Animal damage	
Moose	21.6
Squirrel	12.6
Hare	0.8
Deer	0.8
Porcupine	0.5
Disease damage	
Lophodermella needle cast, <i>Lophodermella concolor</i>	all

Table 2 (continued)

Damaging agents	Percentage of trees affected
Western gall rust, <i>Endocronartium harknessii</i>	19.1
Comandra blister rust, <i>Cronartium comandrae</i>	31.8
Stalactiform blister rust, <i>Cronartium coleosporioides</i>	5.0
Lodgepole pine dwarf mistletoe, <i>Arceuthobium americanum</i> Nutt. ex Engelm.	2.3
Atropellis canker, <i>Atropellis piniphila</i> (Weir) Lohman & Cash	1.2
Dothistroma needle blight, <i>Dothistroma septosporum</i> [Dorog.] Morelet	0.2
Insect damage	
Lodgepole pine terminal weevil, <i>Pissodes terminalis</i>	38.4
Giant conifer aphid, <i>Cinara spp.</i>	2.0
Northern pitch twig moth, <i>Petrova albicapitana</i> (Busck)	1.7
Mountain pine beetle, <i>Dendroctonus ponderosae</i>	0.9
Engraver beetles, <i>Ips pini</i> (Say) and twig beetles	0.8
Pine needle sheath miner, <i>Zellaria haimbachi</i> Busck	0.3
Abiotic-miscellaneous damage	
Competition	15.3
Fork or pronounced crook	9.9
Suppressed	7.9
Mechanical damage	3.1
Broken top or dead unknown	2.9
Chlorotic	0.3

The total percentage of pine attacked by lodgepole pine terminal weevil remained high at the 2014 assessment, but was significantly lower than in 1996, at 38.4% and 45.7%, respectively (Figure 2). The percentage of pine affected by the three major diseases in the stand, comandra and stalactiform blister rusts and western gall rust, increased significantly over time (t -test, $P < 0.01$) (Figure 2). There was very little change over this 18-year interval in the percentage of pest-free pine, despite stem density increasing due to infill.

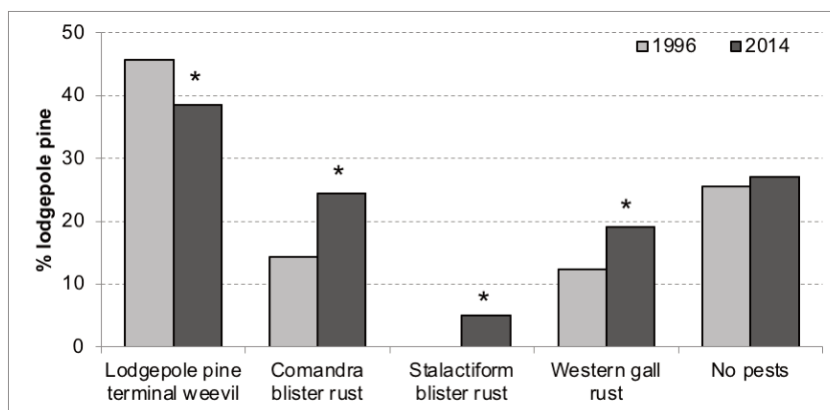


Figure 2. Percentage of lodgepole pine affected by lodgepole pine terminal weevil, comandra blister rust, stalactiform blister rust, and western gall rust, and pest-free trees at two assessment times. The * above bars indicates there was a significant difference in the percentage of pine affected by that pest ($P < 0.01$).

The first attacks by lodgepole pine terminal weevil were recorded in 1981, when trees were very young, about five years old (Figure 3). Attacks per hectare increased dramatically from 1984 through 1992, with a maximum of over 2,500 attacks per hectare in 1985. Attacks by the weevil remained very high but declined from 1992 to 1998. Since 1999, attacks per hectare have been lower but persistent. The lower level of attack is in part due to the smaller, more suppressed infill pines that were added to the plot in 1996 and 1999. These trees had shorter, less suitable leaders and a sub-optimal visual cue for weevils, and therefore sustained fewer attacks than the larger, main plot trees. After 2008, new attacks were often very hard to detect during ground assessments, due to the crowns of plot trees obscuring the view of the terminals.

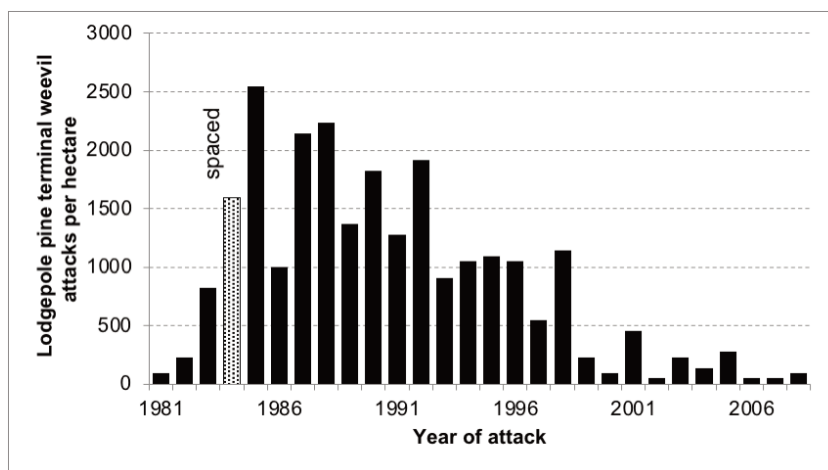


Figure 3. Annual stems per hectare attacked by the lodgepole pine terminal weevil (1981–2008) in the Okanagan Falls plot. Operational spacing was conducted in this stand in 1984.

Often trees sustained more than one weevil attack over their development. Figure 4 illustrates the number of attacks per tree in the 1987 and 2014 assessments. In 2014, just over 50% of trees remained free of any attack by the lodgepole pine terminal weevil. Over 20% of pine sustained one or two attacks, and close to 10% were attacked three or more times by 2014. Even in 1987, 12% of pine had already incurred two attacks (Figure 4). Some trees had evidence of up to six attacks. By 2014, far fewer trees had only one attack than in 1987; conversely, multiple attacks per tree (more than 2) were significantly higher than in 1987.

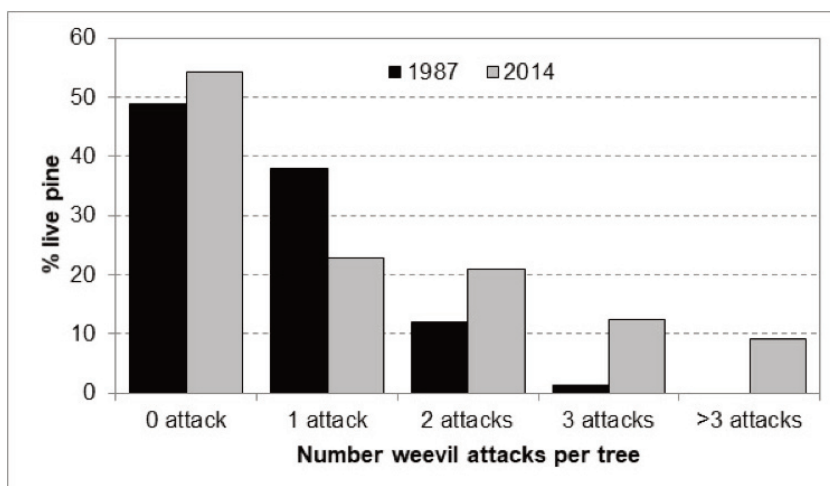


Figure 4. Percentage of live lodgepole pine sustaining no weevil attacks, one attack, two attacks, three attacks, and more than three attacks per tree at the 1987 and 2014 assessments.

The lodgepole pine terminal weevil attacked trees that were less than 1 m to over 9 m in height (Figure 5). The greatest number of attacks occurred when trees were between 1 m and 5 m high. Second and subsequent attacks followed the same trajectory, starting when trees were 1–2 m in height up to 9 m, with the majority of attacks occurring when trees were 2–6 m high. By the final assessment in 2017, over 93% of weevil attacks, and most major defects, had occurred on Layer 1 trees (≥ 12.5 cm DBH; > 1.3 m height) and only 7% were in the suppressed understory canopy (Layers 3–4).

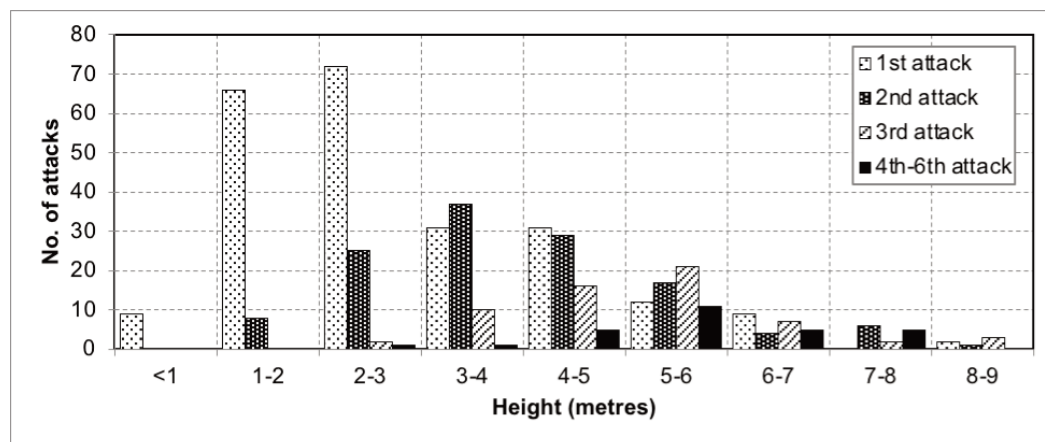


Figure 5. Number of attacks by the lodgepole pine terminal weevil by tree height.

By 2014, the majority of Layer 1 lodgepole pine (172 of 228 trees) was affected by one or more pests and trees that were pest-free were predominantly Layer 3 trees (112 of 126 trees) (over 1.3 m height; less than 7.5 cm DBH) classified as suppressed or infill (Table 3). Many of the suppressed (infill) layers are expected to die and those that survive are unlikely to become crop trees. There was no significant difference in height or diameter of pest and pest-free trees occupying Layers 1 and 2, but pest-free Layer 3 trees were significantly shorter than pest-affected trees, at 4.5 ± 0.2 m and 7.0 ± 0.8 m, respectively (Table 3). This illustrates that trees escaping pest damage were very small and suppressed and will most likely be affected by pests in future years if they don't first succumb to suppression.

Table 3. Average height (m) and DBH (cm) (\pm SE) of pest-free and pest-affected lodgepole pines, by layer, in the 2014 assessment.

	Layer	No. of trees	Height (m)	No. of trees	DBH (cm)
			Avg. (\pm SE)		Avg. (\pm SE)
Pest-free	1	56	13.0 ± 0.3	54	18.1 ± 0.3
	2	14	10.4 ± 0.3	14	9.3 ± 0.3
	3	112	$4.5 \pm 0.2^*$	125	3.0 ± 0.2
One or more pests (including <i>P. terminalis</i>)	1	172	12.7 ± 0.1	174	18.1 ± 0.2
	2	11	9.9 ± 0.4	11	11.0 ± 0.5
	3	14	$7.0 \pm 0.8^*$	17	4.0 ± 0.5

* Average height of Layer 3 pest-free and pest-affected trees was significantly different (t -test, $P=0.001$). cm, centimetres; DBH, diameter at breast height; m, metres; SE, standard error. Note: No. of trees varies between height and DBH due to a few trees being missed/not recorded during assessment.

Only 24% of trees remained pest-free by 2014; 35% of trees were affected by at least one pest, while over 5% had more than four pests per tree. The highest number of pests per tree recorded was seven. When the total number of pests per tree was compared to tree form (Figure 6), it became very clear that as soon as there were two or more pests per tree, the form shifted to moderate or poor form; therefore, a strong correlation exists between total number of pests per tree and final tree form (Chi square, $P < 0.0001$). Over 50% of pine had poor form when two or more pests were recorded (Figure 6).

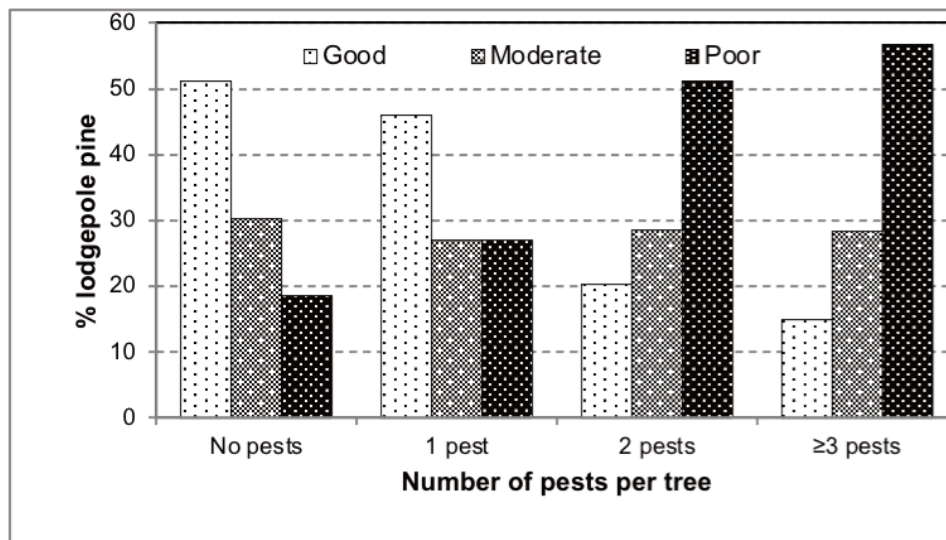


Figure 6. The form (good, moderate, poor) of lodgepole pine not affected by pests or affected by multiple pests at the 2014 assessment.

Over 70% of attacks assessed in 1987, 1993, and 1996 were assessed as major defects (crooks, forks, or stagheads) (Figure 7; Figure 8). Later assessments (1999, 2010, and 2014) saw closer to 50% of attacks classified as minor defects (creases). However, the frequency of forks remained static. Fifty-five percent of attacks occurring prior to 1996 decreased in defect severity, compared to a decrease in severity in only 20% of attacks that occurred from 1996 onward (Figure 9). Very few attacks increased in defect severity from the original classification, whereas the percentage of attacks that remained unchanged from the first assessment prior to 1996 and from 1996 to 2014 was 38% and 76%, respectively.

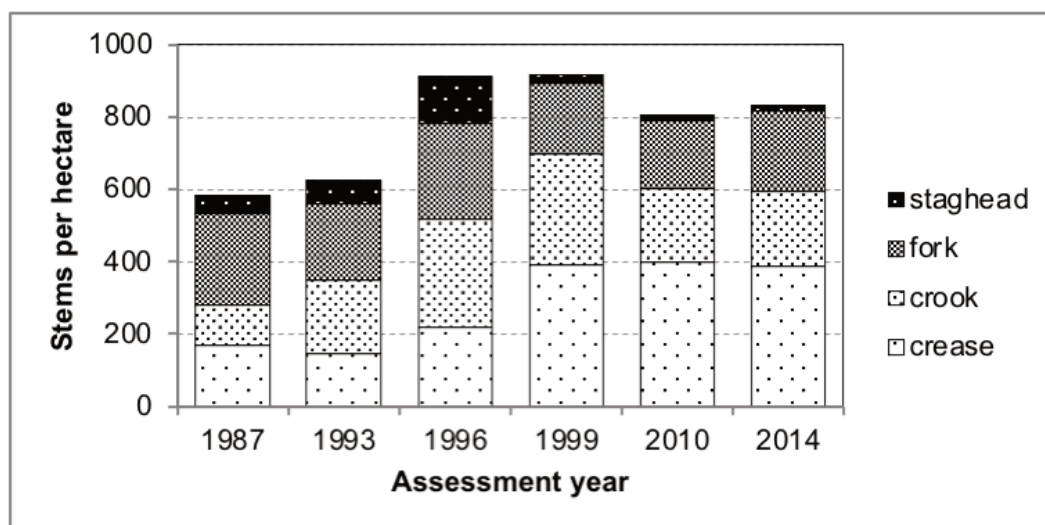


Figure 7. Frequency of defects caused by lodgepole pine terminal weevil attack at six assessment times (1987–2014).



Figure 8. Examples of stem defects caused by lodgepole pine terminal weevil attack. The photograph on the left shows a fork and the photograph on the right shows a staghead with the old leader killed by the weevil still visible in the centre.

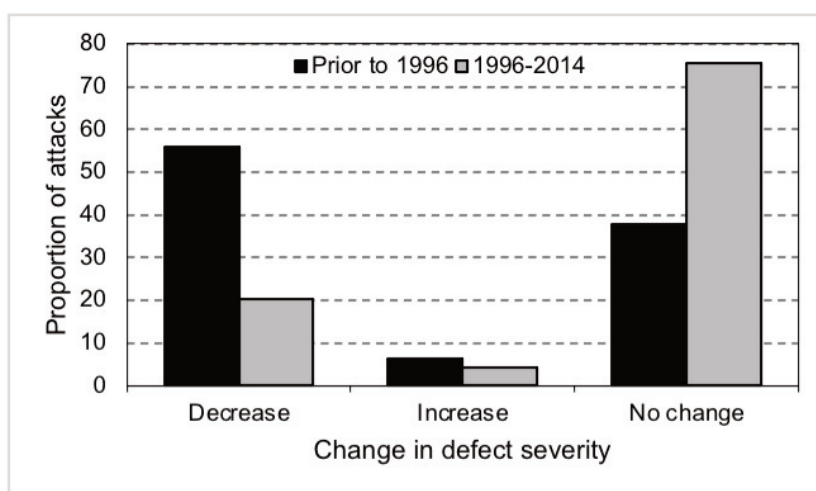


Figure 9. The proportion of defects caused by lodgepole pine weevil attack that decreased, increased, or did not change in severity from the time of first assessment of each attack. Attacks occurring prior to 1996 and from 1996 to 2014 were compared.

The time elapsed (number of years) from when weevil attack first occurred until the 2017 final assessment of defect severity showed a significant correlation (Chi square, $P < 0.0001$). This analysis used all trees and all assessment years. The earlier a tree was attacked in its life, the more severe the defect. The final defect assigned in 2017 to all weevil attacks on live trees was compared to years since attack. There was a significant difference (Chi square, $P = 0.014$) showing that the more years since attack, the more likely a severe defect. The number of weevil attacks per tree over time was highly correlated to tree form (Chi square, $P = 0.0096$). The maximum number of attacks recorded on a tree was six and “poor form” trees had the highest proportion of multiple attacks recorded.

Fifty percent of lodgepole pine in the Okanagan Falls plot was infected or killed by one or a combination of two or three stem rusts (Figure 10; Table 2). Comandra blister rust alone or in combination with other stem rusts affected 936 stems per hectare and western gall rust alone or in combination with other stem rusts affected 595 stems per hectare (Figure 10). The average DBH (\pm SE) of pine when comandra blister rust was first recorded on an individual tree ($N = 113$) was 6.2 ± 0.5 cm. Figure 11 illustrates how co-

mandra blister rust infections increased over time in the stand, with stem and branch infections predominating in 1996 and 1999. In the 2010 and 2014 assessments, most infections (99%) had caused mortality or were recorded as stem infections.

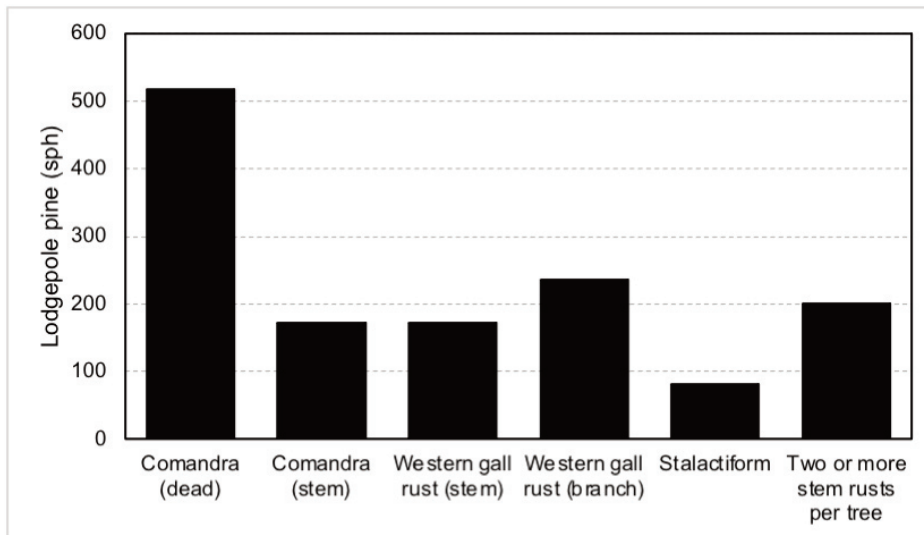


Figure 10. Stems per hectare lodgepole pine affected by one or a combination of stems rusts (live and dead).

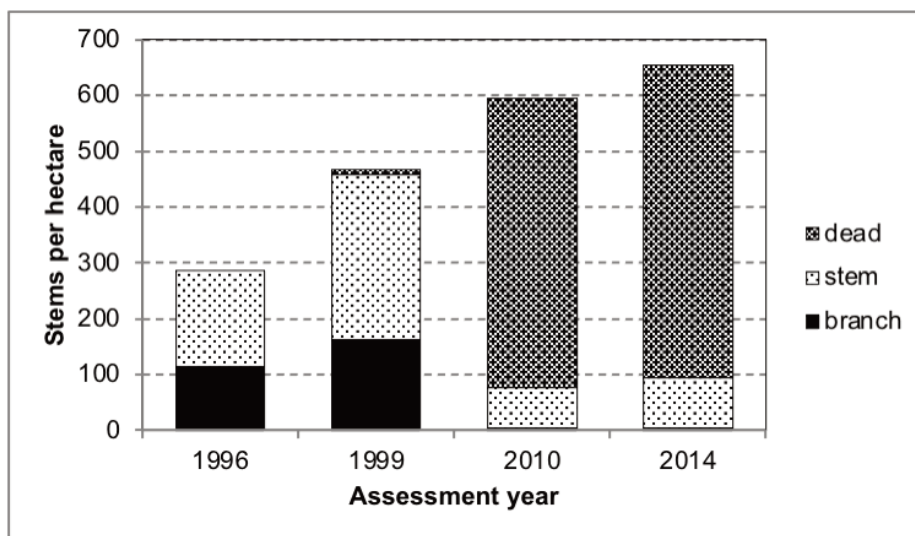


Figure 11. The frequency of lodgepole pine trees infected by comandra blister rust over time (1996–2014). The number of stems per hectare killed or with branch or stem infections is depicted for each assessment year.

Animals also caused damage to trees (Table 2) with squirrel and hare having the most severe impact. Moose and deer browsed on branches and small understory trees causing minimal damage to crop trees. The final form of trees, as recorded in 2017, was compared to the presence of squirrel and/or hare damage. The Chi square tests were all highly significant ($P < 0.001$), showing a strong relationship between animal damage and final form. Almost 60% of trees with squirrel and/or hare damage were classed as poor form and were often affected by other pests such as stem rusts.

Assessing tree form using the number and diameter of branches at DBH showed that average branch diameter was an important variable in determining form (Table 4) of Layer 1 trees, whereas the average number of branches was less important. In the Okanagan Falls plot, trees exhibiting poor form had significantly larger branch diameter (3.0 ± 0.1 cm) than those having moderate or good form (2.4 ± 0.1 cm and 1.3 ± 0.1 cm), respectively.

Table 4. Tree form in Layer 1, 2, and 3 trees, and the average number (\pm SE) and diameter (\pm SE) of branches at DBH.

Layer	Form	N	Avg. no. branches \pm SE ^a	Avg. branch diameter at DBH \pm SE ^a (cm)
1	good	20	4.2 \pm 0.2a	1.3 \pm 0.1a
	moderate	100	4.8 \pm 0.1b	2.4 \pm 0.1b
	poor	112	4.7 \pm 0.1ab	3.0 \pm 0.1c
2	good	15	3.9 \pm 0.2	0.8 \pm 0.1
	moderate	1	3	2.8
	poor	1	4	1.2
3	good	19	3.3 \pm 0.3	0.6 \pm 0.03
	moderate	9	3.6 \pm 0.3	0.8 \pm 0.2
	poor	2	2.5 \pm 0.5	0.5 \pm 0.1

cm, centimetre; DBH, diameter at breast height; SE, standard error. ^a The same letter following averages of Layer 1 trees indicates no significant difference (ANOVA $P < 0.05$; Tukey's test).

Discussion

Of the 17 plots established throughout the southern interior of British Columbia between 1985 and 1991, only one plot was highlighted in this study in order to discretely follow more than 600 individual trees, and the pests affecting each tree, through numerous assessments over a 30-year period. This analysis will lay the groundwork for summarizing the results of the full 17-plot study. This study clearly shows how a young lodgepole pine stand develops and is influenced by pests during its first 40 years of growth. Considering the depth of study and length of tree development studied in this plot, results may indicate patterns for lodgepole pine vulnerability and growth response to pests in the region. Pine density changed from 1,295 sph in 1987 to 1,686 sph in 2017. However, over this 30-year assessment period, almost 1,000 pine died and only 1,041 were classified as Layer 1 trees (dominant or crop trees) by the final assessment. The other 38% of lodgepole pine in the plot (Layer 2 and 3 trees) were highly suppressed, primarily infill, and are unlikely to become crop trees. During this formative time in stand development, 25 different damaging agents were recorded affecting trees in the stand—more than were reported by Heineman et al. (2010) and only 24% of Layer 1 trees remained pest-free compared to 68% of stems examined by Humphreys & Van Sickle (1992) in their study. Lodgepole pine terminal weevil and stem rusts were commonly found in both studies (Humphreys & Van Sickle 1992, Heineman et al. 2010). Lodgepole pine terminal weevil had the highest incidence of all pests recorded, affecting over 38% of the lodgepole pine, many of which suffered up to six attacks. This insect is found throughout much of the range of lodgepole pine in Canada and the USA (Drouin et al. 1963, Maher 1981, Bella 1985 Cameron & Stark 1989, Heineman et al. 2010) and currently has exponentially more susceptible resource available for attack because of the recent surge in salvage harvesting and reforestation efforts (Fletcher 2018) due to MPB and wildfires. Annual weevil attacks per hectare increased rapidly from about age eight to 20 years, before tapering off as trees reached 25 years and were over 6 m in height. Many trees sustaining weevil attack over this 30-year assessment period died from other causes, but the majority of surviving Layer 1 dominant trees incurred one or more attacks, leading to major defects and poor form. The greater the number of attacks per tree and the more time since the attack had occurred increased the likelihood of severe defect formation and poor tree form. Half the attacks monitored on the remaining live lodgepole pine in the plot resulted in severe defects.

Early on during stand development, when the pine was less than 20 years, 56% of defects caused by weevil attack decreased in severity, while 38% remained unchanged from the initial assessment. However, these initial defect assessments included many severe category defects. Attack levels increased rapidly in early stand development and the majority of defects were severe (crooks, forks, stagheads). Attacks on shorter trees are more likely to cause severe stem defects and significantly compromise the future value of the tree. When trees are small, with long, thick leaders, they are very attractive to weevils, being highly visible and receiving optimum light and warmth for weevil development (Maclauchlan & Borden 1996). As trees continue to develop, from age 20 years onward, defects from weevil attacks are less likely to decrease in severity from the initial assessment. In this study, once trees were over 21 years, 76% of defects caused by weevil attacks saw no change from their initial evaluation, and about half of the defects were still categorized as severe.

At low initial stand densities, or when spacing is conducted early in stand development, there is an increase in the severity of defects due to weevil attack (Alfaro & Omule 1990, Maclauchlan & Borden 1996). Later in stand development, when trees are taller and at least 20 years in age, attacks persist, but often result in less severe defects. Early attacks that form severe stem defects are the most detrimental to tree form and quality because they are located on the most valuable portion of the tree (the first log) (Alfaro & Omule 1989, Jozsa & Middleton 1994, Weyerhaeuser Company Limited, pers. comm.). Similar to attacks by the Sitka spruce weevil on spruce, repeated leader destruction leads to stem deformities, which reduces a tree's value and options for potential end use (Alfaro 1989). The degree to which stem defects and form affect tree quality, waste (cutting out defects), and value depends on the end use and processing of trees (Jozsa & Middleton 1994). Forks make up about 20% or more of defects caused by weevil attack and are particularly damaging because they cause a defect at the attack origin and divide the tree's resources between two or more stems, depending on the number of times the tree forks due to multiple weevil attacks. Stem density post-spacing was low in the Okanagan Falls stand and this fact was reflected in the severity of defects caused by the weevil. The regeneration of lodgepole pine stands at higher densities and the maintenance of these densities throughout early stand development may reduce the severity of attacks but will likely not affect the total number of attacks.

Hard pine stems rusts were recorded on 50% of stems alone or in combination, with comandra blister rust causing the greatest amount of mortality and western gall rust severely impacting both tree form and mortality. Over 850 stems per hectare were killed by comandra blister rust alone or in combination with other pests, such as western gall rust and squirrel feeding on infections (Sullivan & Sullivan 1982). Western gall rust can cause serious growth loss or mortality (Geils & Jacobi 1990, Woods et al. 2000) and both diseases, as well as stalactiform blister rust, can cause stem defects that result in poor form (Ziller 1974, van der Kamp & Spence 1987, Hiratsuka et al. 1988, van der Kamp 1994). Generally, branch infections are less damaging than stem infections, but may grow into the main stem, causing tree death (van der Kamp 1994, Woods et al. 2000).

As mature forests in British Columbia are increasingly converted to young, regenerating forests through natural disturbances, such as insects, disease, or fire (Pojar 2010, FLNRORD 2019) or planned harvesting operations, ensuring that young stands are healthy is imperative to achieving land managers' goals and objectives. The impacts of climate change on some insects, disease, and young stands are already evident (Woods et al. 2000, Allen 2009, Pojar 2010, Woods et al. 2010, Ramsfield et al. 2016, Woods et al. 2017, Maclauchlan & Buxton 2019) and we anticipate these impacts will become more

prevalent and severe in the future. Lodgepole pine terminal weevil was one of the most prominent and damaging pests in this study. The *Pissodes* genus is very responsive to temperature (Sullivan 1961, Maclauchlan & Brooks 2000, Sieben 2000) and as our climate warms, it will adapt to longer growing seasons and attack incidence will likely increase. More open-grown stands will allow more warmth for weevil development and will promote a branchy tree form; therefore, it is important to maintain higher densities at early stand development and be mindful of treatment entries over the development of stands. Woods et al. (2005) related increased decadal summer precipitation and increasing climate-related tree stresses with an unprecedented outbreak of *Dothistroma* needle blight (*Dothistroma septosporum* [Dorog.] Morelet) in central British Columbia.

More recently, in 2018, Maclauchlan and Buxton (2019) recorded drought damage and mortality on over 118,000 hectares in the Thompson Okanagan Region, much of this in young pine, with associated secondary mortality attributed to insects, disease, and animal damage that were already resident in stands. The Okanagan Falls study quantified and described the impact of pests over the early stage of lodgepole pine development and the results were unequivocal in terms of the detrimental effects on both survival and form. The interaction of pests, cumulative attacks by single pests, and periodic surges in pest occurrence all play a role in drastically impeding the desired stocking and form of pine. The most damaging pests recorded in the Okanagan Falls plot were lodgepole pine terminal weevil, comandra blister rust, and western gall rust, which are ubiquitous throughout regenerating lodgepole pine (Bella 1985, Cameron & Stark 1989, Humphreys & Van Sickle 1992, Woods et al. 2000, Heineman et al. 2010).

Most other studies look at a point-in-time assessment of the incidence or geographic range of the pests (Bella 1985, Humphreys & Van Sickle 1992, Woods et al. 2000, Heineman et al. 2010) rather than the compounding effects of pest damage over time. Incidence surveys are valuable as they indicate patterns over a landscape and provide valuable information as to where more intense monitoring may be needed. However, both incidence and impact data are required to make accurate forest yield projections for mid- and long-term timber supply modelling. Cumulative pest impacts on our forests will be exacerbated in the future (Allen 2009, Ramsfield et al. 2016) and there will be increased demand from this ever-shrinking resource. Therefore, it is critical to incorporate these long-term impacts into our management goals and expectations. This can only be achieved by having many widespread permanent installations that track individual damaging agents over the life span of trees and stands. In British Columbia, there are two types of long-term monitoring conducted by the Ministry of Forests, Lands, Natural Resource Operations and Rural Development: Young Stand Monitoring plots and the Permanent Sample Plot network, both of which are widespread throughout the province and re-measured at regular intervals. These installations provide an opportunity to gather more information on damaging agents affecting British Columbia's forests. There is evidence that the incidence of pest damage in stands is higher now than two decades ago (Maclauchlan 2020) possibly due to changed climatic conditions, which would translate into lower quality trees and possibly lower yields.

These findings emphasize the need for continued and augmented monitoring and assessment of damaging agents affecting the development of young stands. In these times of climate compromise, we must clearly articulate the management goal for each stand, whether for carbon sequestration, habitat, or fibre, and develop a plan for the harvest, site preparation, species selection, and stand tending to meet these goals and identify risks that may impede these objectives.

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