Forest health and mortality of advance regeneration following canopy tree mortality caused by the mountain pine beetle

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Mountain Pine Beetle Working Paper 2010-03

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PBP Project # 7.25

Abstract

British Columbia is amid the largest recorded mountain pine beetle outbreak in North American history. To minimize timber losses, large-scale salvage operations are underway to utilize the merchantable pine. However, large-scale salvage operations can have negative impacts on a variety of forest values, including the potential to diminish mid-term timber supply opportunities. One option is to reserve stands with adequate advance regeneration for the mid-term timber supply. Another option is to salvage harvest dead trees in a way that protects the advanced regeneration. However, the health, vigour, form, and mortality rate of advance regeneration, through time, has not been well studied. To incorporate these stands into timber supply analyses and subsequent management decisions regarding reservation, mortality and forest health factors must be evaluated. We assessed the forest health of 90 residual stands over a range of stand types with varying lengths of time since attack by mountain pine beetle (MPB). Analysis of the forest health survey data showed that current damage from forest health agents was relatively low. Physical damage was the most common issue, but even in that case, the incidence ranged from < 1 to 5.5% of trees grouped by species. Forest insects and pathogens that were common in the overstorey, either at the time of sampling or before MPB mortality, have the most potential to cause future damage. These agents included dwarf mistletoe and root diseases. Both of these agents spread from overstorey to understorey and can intensify throughout the life of the stand. Foliar pathogens and insects were low in incidence and are not expected to increase over the next rotation. However, they have the potential to increase in severity with climate change and should be monitored closely. Tree ring analysis showed a strong release in growth of advanced regeneration that was timed with overstorey mortality. The magnitude of the response was related to the proportion of the overstorey that was pine compared to non-host species, and was not related to the species of understorey tree.

Keywords: advanced regeneration, mountain pine beetle, growth release, time since death

Résumé

La Colombie-Britannique est aux prises avec la plus grave infestation du dendroctone du pin ponderosa de l'histoire de l'Amérique du Nord. Des coupes de récupérations à grande échelle y sont en cours afin de récolter le bois de pin marchand et de réduire au minimum les pertes de bois de sciage. Or, de telles opérations à grande échelle peuvent avoir des impacts négatifs sur diverses valeurs de la forêt et risquent notamment de réduire l'approvisionnement en bois à moyen terme. Une des options consiste à garder en réserve des peuplements à régénération préexistante adéquate pour assurer l'approvisionnement à moyen terme. Une autre option est de récolter les arbres morts tout en protégeant la régénération préexistante. Cependant, peu d'études ont portés sur la santé, la vigueur, la forme et le taux de mortalité de la régénération préexistante au fil des ans. Pour incorporer ces peuplements aux analyses de l'approvisionnement en bois et aux décisions d'aménagement ultérieures concernant les réserves forestières, il faut évaluer les facteurs liés à la mortalité et à la santé des forêts. Nous avons évalué la santé de 90 peuplements résiduels de types divers et attaqués depuis plus ou moins longtemps par le dendroctone du pin ponderosa (DPP). L'analyse des données de l'enquête sur la santé des forêts a révélé que les forêts étaient relativement peu endommagées par des organismes nuisibles à l'heure actuelle. Les dégâts physiques étaient le problème le plus courant mais même dans ce cas, leur fréquence oscillait entre < 1 et 5,5 % des arbres groupés par essences. Les insectes et maladies des arbres qui étaient répandus dans l'étage dominant soit au moment de l'échantillonnage ou avant la mortalité causée par le DPP, risquent fort bien de causer les futurs dégâts. Parmi les agents pathogènes figurent le faux-gui et les pourridiés. L'un et l'autre se propagent depuis l'étage dominant jusqu'au sous-étage et peuvent s'aggraver dans un peuplement au fil du temps. Les insectes et les maladies du feuillage étaient peu fréquents et ne devraient pas augmenter au cours de la prochaine révolution. Ils risquent toutefois de causer des dégâts plus graves sous l'effet du changement climatique et devraient être surveillés de près. L'analyse dendrochronologique a révélé une forte reprise de la croissance de la régénération préexistante qui a coïncidé avec la mortalité de l'étage dominant. L'ampleur de la réaction était corrélée à la proportion de l'étage dominant constituée de pins plutôt que d'essences non hôtes mais non pas aux essences du sous-étage.

Mots clés: régénération préexistante, dendroctone du pin ponderosa, reprise de croissance, temps écoulé depuis la mort

Contents

List of Tables

List of Figures

1. Introduction

British Columbia is amid the largest recorded mountain pine beetle (*Dendroctonous ponderosae* Hopkins; MPB) outbreak in North American history. The epidemic has caused widespread mortality of lodgepole pine, the province's most abundant commercial tree species. It has been estimated that by 2020, 67% of the province's mature pine will have been killed by the beetle (Canadian Forest Service 2010). In order to minimize timber losses, the Chief Forester of British Columbia has increased the Allowable Annual Cut (AAC) in affected areas, allowing for large-scale salvage of merchantable timber.

Due to such salvage efforts, resource managers have been forced to rethink which trees and stands should be cut, when and where, and which ones should be left behind. It is not possible or desirable to harvest all affected pine forests (Eng 2004). Poorly planned and executed large-scale salvage operations can have negative impacts on a variety of forest values, including hydrology, visual quality, and wildlife habitat. In addition, salvage initiatives have the potential to diminish mid-term timber supply opportunities. The mid-term is generally defined as the time when the accelerated AAC is adjusted downward from the present uplifts. Coates et al. (2006) found that approximately 40–50% of pine-leading stands in north central British Columbia have sufficient advance regeneration densities to be stocked without further silvicultural intervention. Further, they suggest that such understorey trees, if protected, could reduce rotations by 10–30 years compared to complete salvage and planting (Coates et al. 2006).

Current guidance on the topic offers the following solutions: 1) pure lodgepole pine stands should be considered preferred candidates for immediate harvest over mixed species stands; 2) stands with a shorter shelf life should be harvested soonest; and 3) stands with a viable advance regeneration component should be left unharvested to provide, among other values, mid-term timber supply opportunities.

Following MPB attack, relying on advance regeneration to provide mid-term timber supply opportunities, however, remains an uncertain management option with unknown implications. For example, the health and vigour of advance regeneration will directly influence its growth rates post MPB. Advance regeneration may also have poor form (e.g., tree-fall scars and decay in advance regeneration), rendering them unacceptable for timber objectives. Eventually, biotic and abiotic stresses that result after a stand has been attacked by MPB may cause significant mortality of advance regeneration. Combined, these unknown factors can diminish the viability of the residual stand as a mid-term timber supply opportunity. To incorporate stands with viable advance regeneration into timber supply analysis and subsequent management decisions regarding the reservation of such stands, mortality, health, vigour, and form of advance regeneration must be evaluated.

1.1 Project Objectives

The overall purpose of this project was to assess the forest health of residual stands over a range of stand types with varying lengths of time since attack by MPB. Specific objectives were:

1. Determine the existing biotic and abiotic forest health agents that pose significant threats to stand regeneration via advance regeneration under current climatic scenarios;

2. Identify potential biotic and abiotic forest health agents that pose significant threats to stand regeneration via advance regeneration under predicted future climatic scenarios;

3. Quantify mortality of advance regeneration by forest health agent where possible;

4. Determine whether or not the health, vigour, and form of remaining advance regeneration are sufficient to consider the remaining stand stocked without further silvicultural intervention; and

5. Quantify the levels of decay in advance regeneration due to tree-fall scarring.

2. Methods

2.1 Sampling Area

Sampling took place within the Prince George, Vanderhoof, and Nadina Forest Districts. Across the three districts, sampling included the dry-warm, dry-cool, and moist-cold Sub-boreal Spruce Biogeoclimatic subzones (SBSdw3, SBSdk, and SBSmc, respectively; Figure 1). Within each subzone, 30 previously pine-leading stands with sufficient advance regeneration to reasonably expect a mid-term harvest opportunity were selected randomly from a set of candidate stands that met the following selection criteria:

- pre-beetle pine-leading: sub-canopy and canopy tree composition (measured by percent basal area) was greater than 50% pine;

- sufficient advance regeneration: minimum threshold of 1000 stems per ha (sph) to represent a stocking level that should result in full site occupancy by advance regeneration (Coates et al. 2006), or as per *Regulation for Protecting Secondary Structure* from the Forest Practices and Planning Reg. 43.1 (BC Ministry of Forests and Range 2004); and

- accessible by road.

2.2 Field Data Collection

For the first 20 sites in each subzone, 5 plots were measured, and for the remaining 10 sites in each subzone, 3 plots were measured for a total of 130 plots per subzone. Plot centres were spaced 50 m apart and were located from a convenient tie-point along the access road, using a randomly selected bearing. Plots were sampled using procedures developed by Coates et al. (2006). Advance regeneration at each plot was stratified into the following classes:

- established seedlings (10 cm to less than 1.3 m tall);

- saplings (1.3 m tall to < 7.5 cm diameter at breast height [dbh], measured 1.3 m from the ground);

- sub-canopy (7.5 cm dbh to < 15.0 cm dbh); and

- canopy trees (15.0 cm dbh and greater).

Seedlings and saplings were tallied in a 1/200 ha plot, and canopy trees in a 1/50 ha plot. For each advance-regeneration class, all live and dead trees were counted, species identified, classed as either live or dead, and if dead the mortality agent was determined, if possible.

Crop trees (healthy, well-spaced) were selected at each plot and determination of the free-growing status[1] of each plot was made using Provincial Stocking Standards (Prince George Forest Region) for the appropriate subzone (BC Ministry of Forests and Range 2010). Growth increments were measured using one of two methods for each crop tree. Vertical increment over

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[1] An area is considered to be free-to-grow when the regenerating trees are free of reasonably foreseen impediments to growth.

the past one year and five years was measured using a tape measure, or radial increment was measured by taking a disc or an increment core of the crop tree.

To determine the time since attack for each stand, two dead dominant lodgepole pine trees at each plot were cored at 1.3 m above ground using an increment borer.
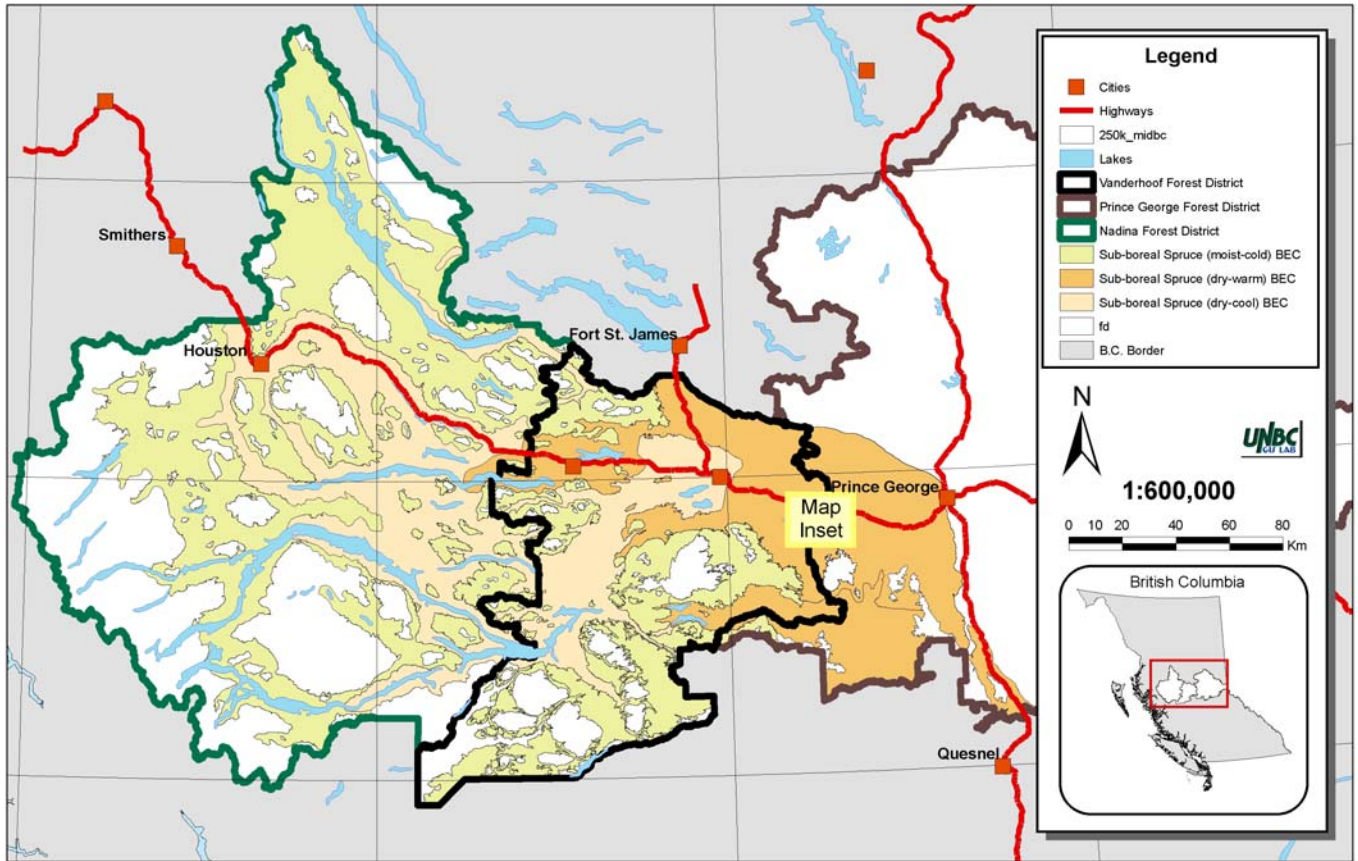
Figure 1. SBSdk, SBSdw3, and SBSmc subzones found in the Prince George, Vanderhoof, and Nadina Forest Districts.

2.3 Tree Ring Analysis

All collected discs and cores were prepared for radial growth measurement using procedures of Stokes and Smiley (1968). Discs and cores were sanded using progressively finer grits of sandpaper. Radial growth measurements were made using a Velmex measuring station (Velmex, Inc. 1992) in conjunction with Measure J2X (Voortech Consulting 2004). To determine the mortality date of the overstorey lodgepole pine, cores from dead lodgepole pine were cross-dated against a local master chronology (Lewis and Thompson 2009) with the assistance of the computer program COFECHA.

Radial growth response of crop trees to overstorey mortality was assessed using the computer program JOLTS, which identifies increases in growth that meet user-defined criteria, which in this case included a 50% growth increase with a 5-year window before and after release. Radial response was also assessed visually from graphs of individual tree growth over time.

2.3 Data Analysis

Biotic and abiotic agents of damage identified during the sampling were grouped into tables and figures by subzone and tree species. For some analyses, the SBSmc2 and SBSmc3 variants were analyzed separately, and for some they were combined due to sample size.

Vertical growth responses of crop trees among species for the last year's growth and the last five years' growth were analyzed using ANOVA. Analyses were done separately for each of the four subzones/variants due to differences in species composition.

Percent trees releasing within one year before and four years after the main mortality year for each stand were plotted by subzone. Trees releasing one year prior to the main mortality year were included because in most stands overstorey pine were killed by mountain pine beetle over several years, therefore the crown would start to thin in most stands prior to the main mortality year.

Regeneration health, vigour, and form were compared against the stand-level time since attack and the degree of pine mortality.

3. Results

Table 1 shows the breakdown of sites and plots by subzone, and the overall tally of understorey and canopy trees.

Table 1. Sites and plots by subzone, and the number of understorey trees (seedlings and saplings) and canopy trees.

| Subzone	No. Sites	No. Plots	No. Understorey Trees					No. Canopy Trees				
			Bl	Sx	Sb	Pl	Fd	Bl	Sx	Sb	Pl	Fd
SBSdw3	30	130	464	395	68	96	352	128	869	126	2111	208
SBSdk	30	130	116	355	325	466	0	12	529	119	2695	0
SBSmc2	5	25	303	74	157	33	0	109	40	43	622	0
SBSmc3	25	105	306	193	666	228	0	121	568	271	2070	0

Note: Understorey trees are seedlings and saplings up to 7.5 cm diameter, and canopy trees are trees greater than 7.5 cm diameter. Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir.

3.1 Abundance and Condition of Seedlings and Saplings

The only subzone with Douglas-fir in the understorey was the SBSdw3, where Douglas-fir was a dominant component of the seedling layer in the understorey (353 sph), along with subalpine fir (349 sph).The sapling layer in the SBSdw3 was dominated by subalpine fir (335 sph) and interior spruce (361 sph). The SBSdk was dominated by lodepole pine in both the seedling (383 sph) and the sapling layers (349 sph). The wettest subzone, the SBSmc had the most black spruce in the seedling layer (972 sph), with subalpine fir the second most common (664 sph) (Figure 2).

Most of the understorey trees were in a healthy condition. The most common abiotic problem was curved stems (sweep), which was most frequent in the two spruce species. Other abiotic damage was limited to less than 3% of trees being attacked for all species (Figure 3a, b). In terms of damage caused by biotic agents, browsing and other forms of injury caused by animals (vertebrates) was by far the most common compared to damage caused by fungal or insect agents. Animal damage was consistent across all subzones, with subalpine fir being the most seriously affected, followed by spruce species. Lodgepole pine was least susceptible to damage by animals (Figure 4). Western gall rust ranged from 2.5 to just over 6% incidence in lodgepole pine. The

only other significant damage presumably caused by fungal agents was cankers (localized areas of necrotic bark) for which no causal agent could be identified. These were particularly prevalent in the SBSdw3 (Figure 5a, b).
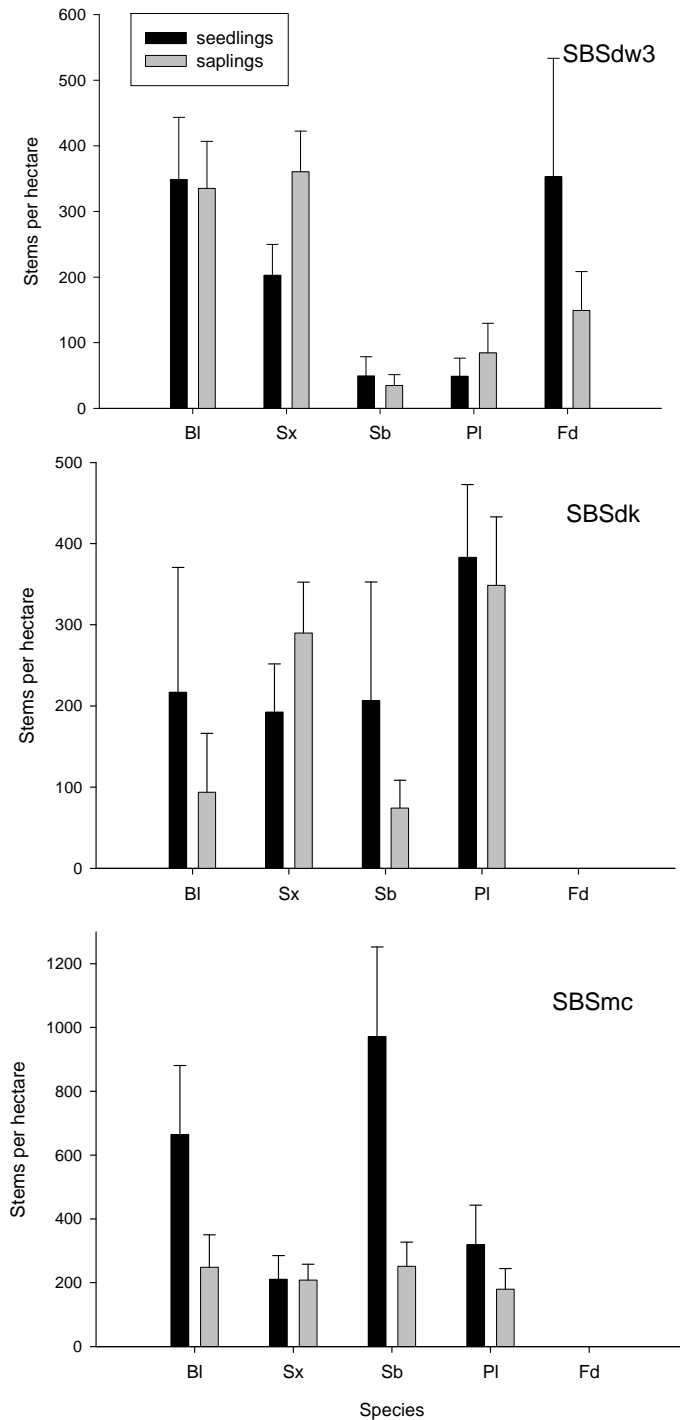
Figure 2. Seedlings and saplings in the understorey of stands in three subzones.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

Figure 3a. Percent seedlings and saplings in the SBSdw3 and SBSdk damaged by abiotic factors.
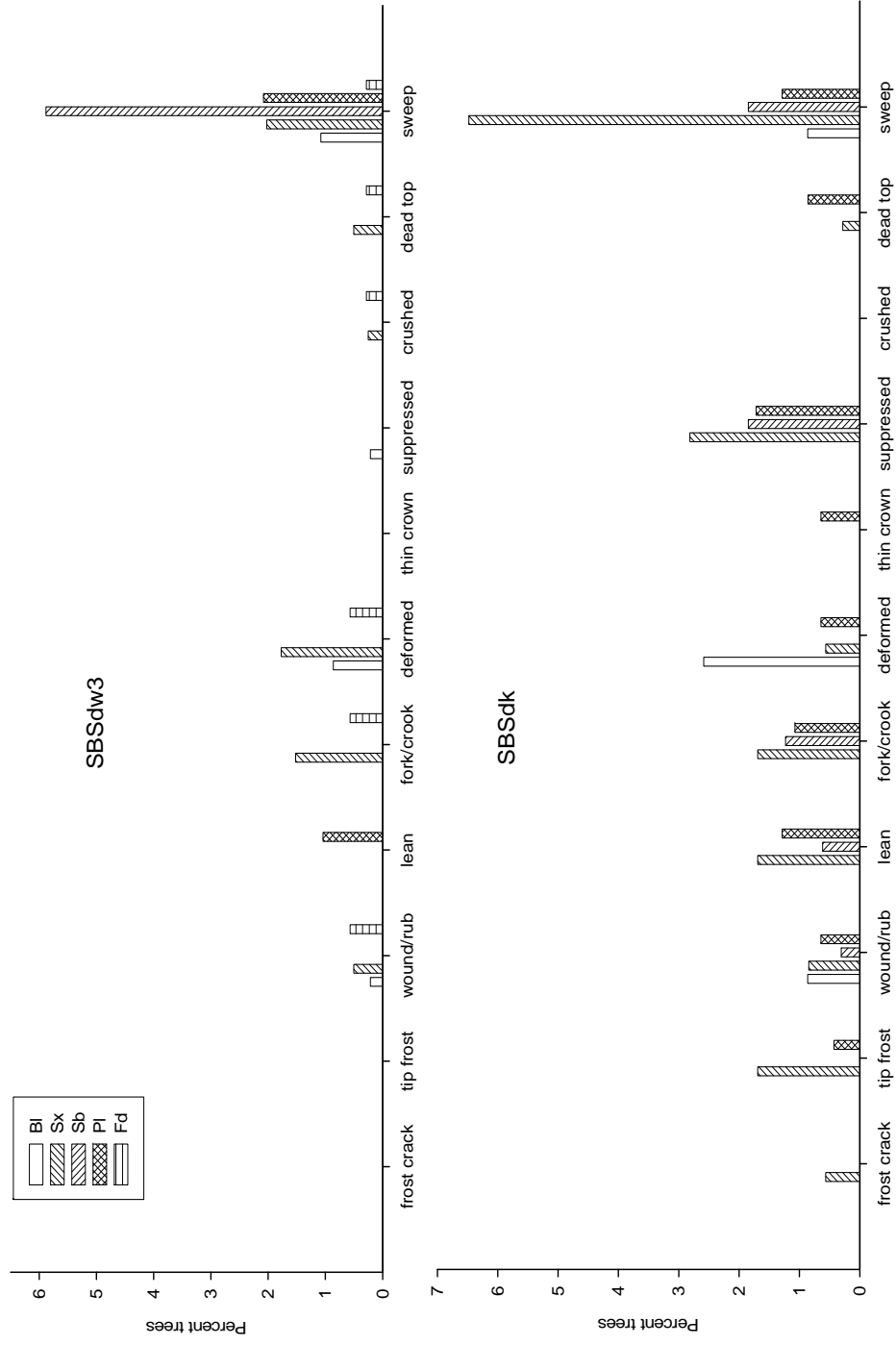(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

6
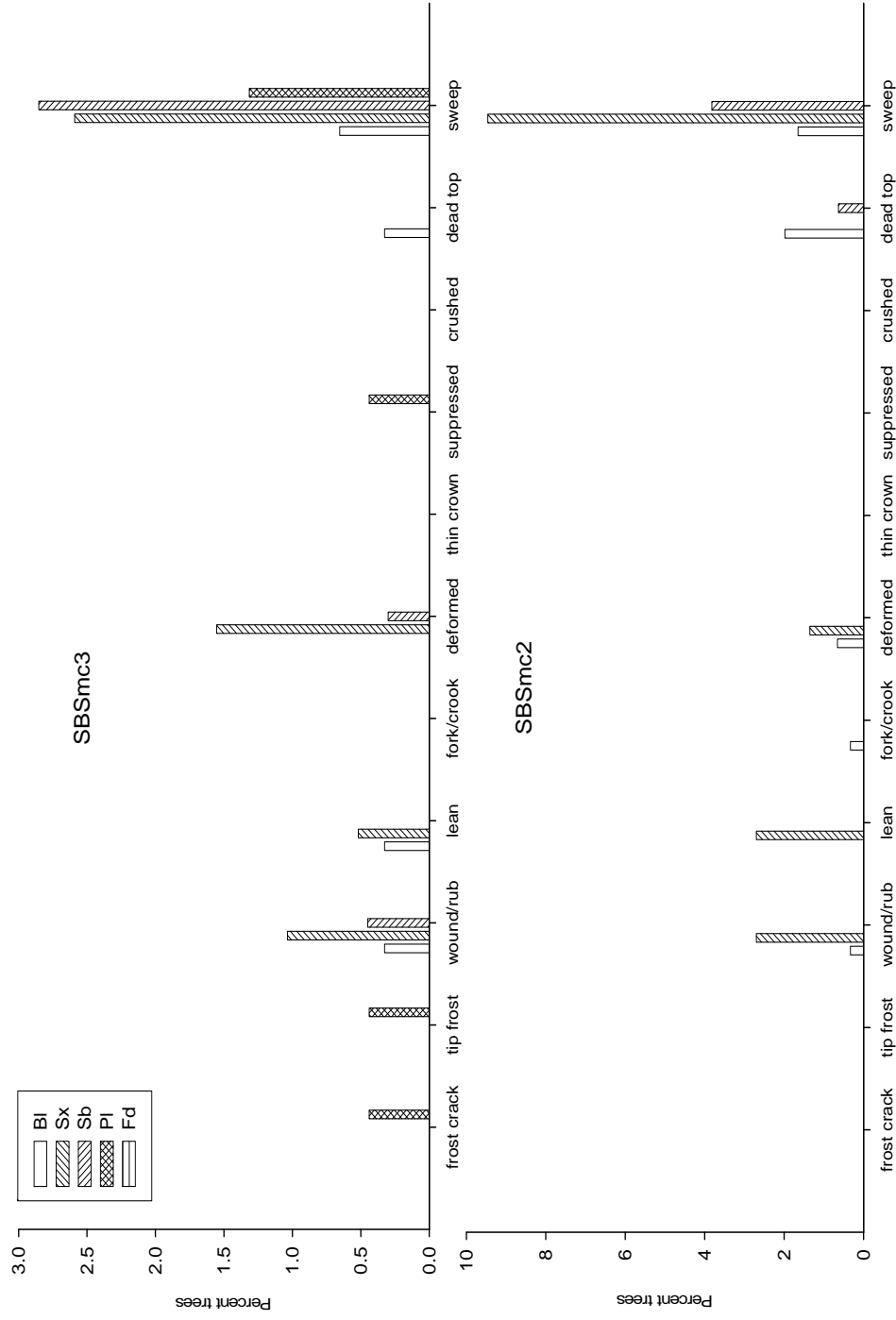
Figure 3b. Percent seedlings and saplings in the SBSmc3 and SBSmc2 damaged by abiotic factors.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

7
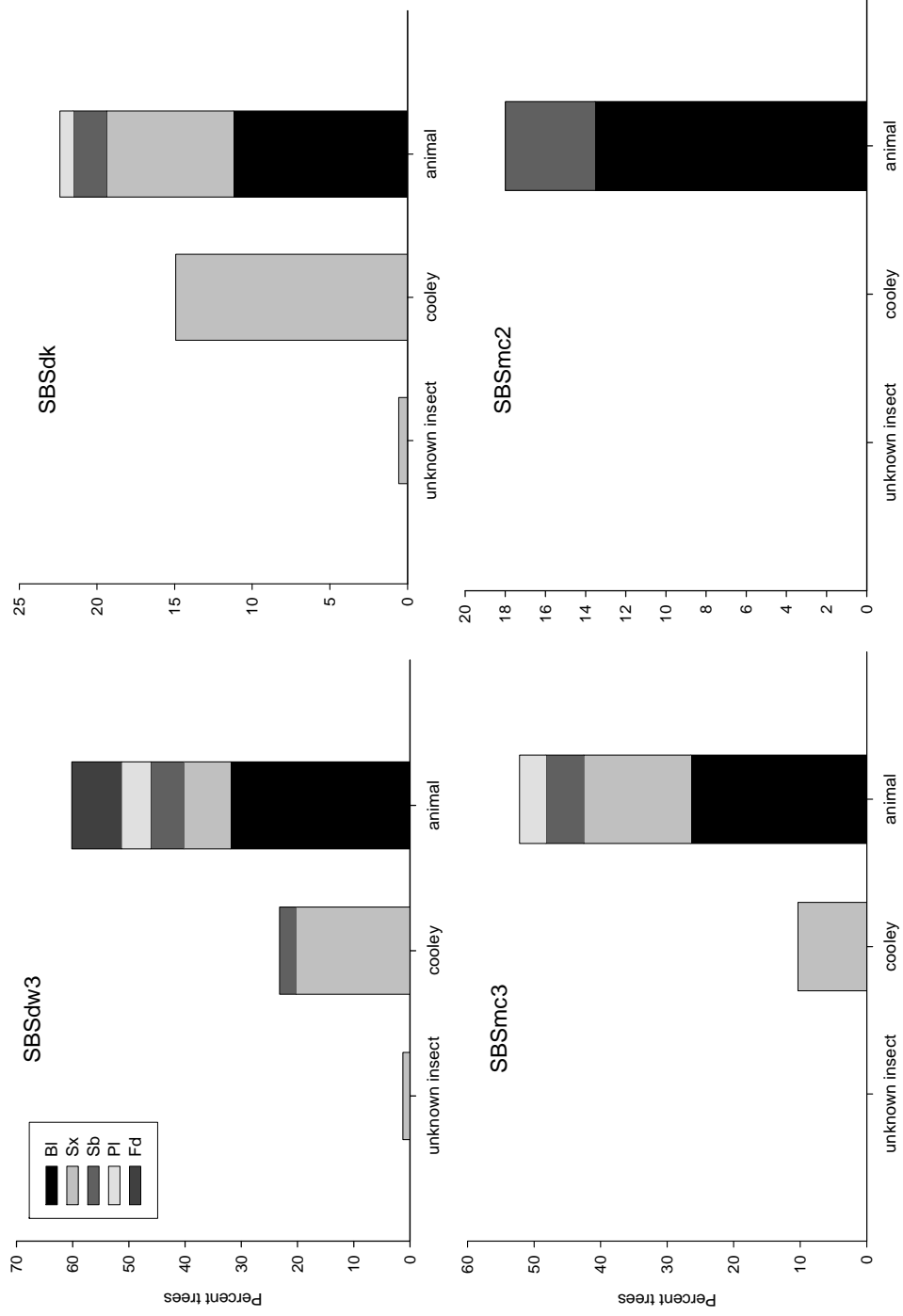
Figure 4. Percent seedlings and saplings affected by biotic agents (insects and animals) in each subzone.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

8

Figure 5a. Stem diseases observed on seedlings and saplings in the SBSdw3 and SBSdk.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

Figure 5b. Stem diseases observed on seedlings and saplings in the SBSmc3 and SBSmc2.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

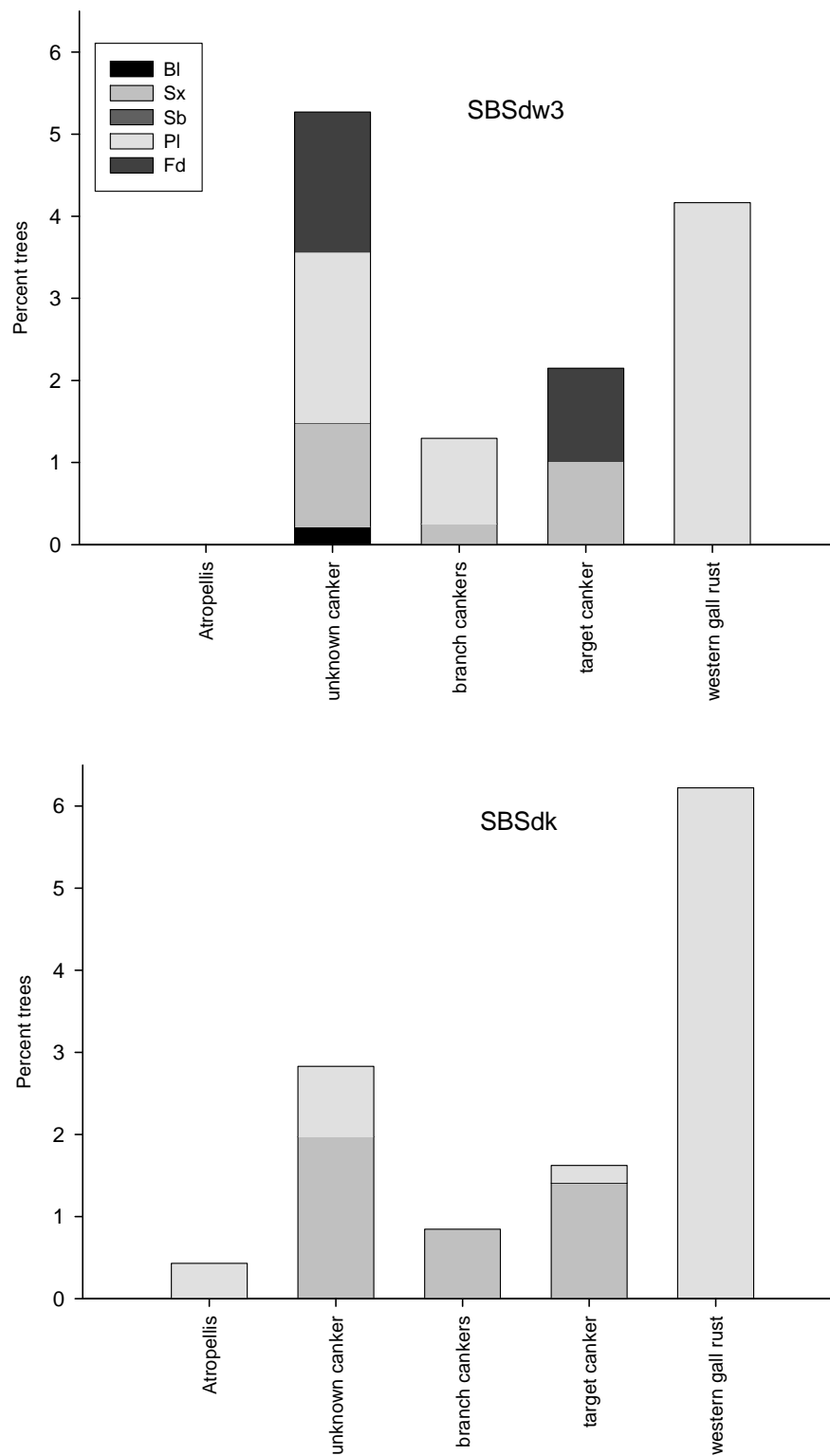## 3.2 Abundance and Condition of Canopy Trees
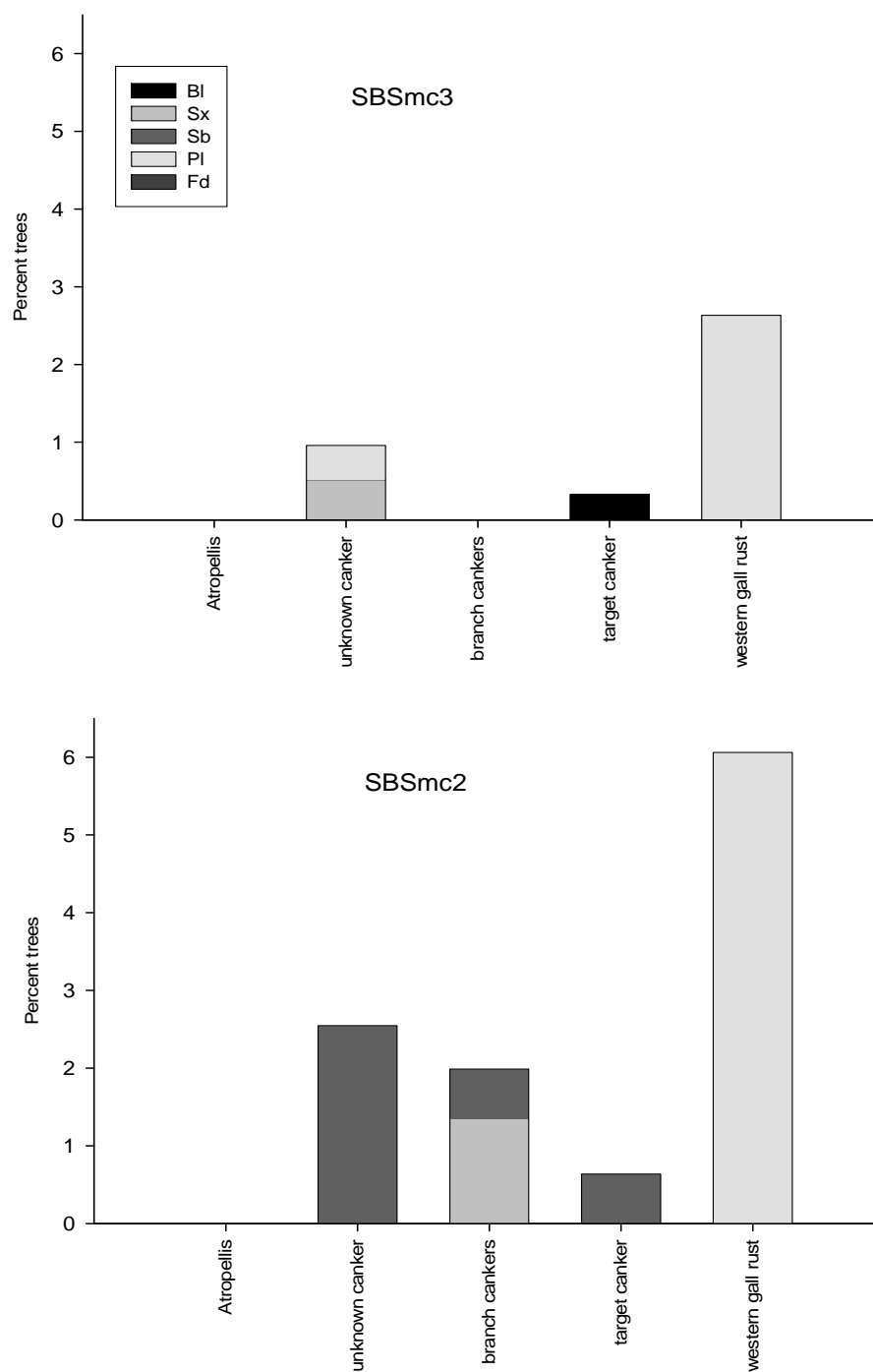
Figure 6 shows the distribution of canopy trees by diameter class and condition (standing live, standing dead, down dead) for each species in each subzone. Most subzones and species show a greater abundance of small diameter trees, with the exception of interior spruce in the SBSmc2. With lodgepole pine, in all subzones dead trees outnumbered live trees (although the SBSmc2 had almost as many live trees as dead), and in all cases, the dead pine that had fallen were predominantly in the smaller size classes (Figure 6a-d).

Tables 2 and 3 list the forest health agents observed in canopy trees. Table 2 has agents that are in one of two categories: have a broad host range or have a narrow host range but can be grouped (e.g., bark beetles). Table 3 lists host specific agents. Bark beetles (mountain pine beetle and spruce beetle) were among the most prevalent forest health agents, followed by root disease (primarily tomentosus root disease on black and interior spruce) and physical damage caused by animals.

3.3 Free Growing Status

For each stand in each subzone, individual plots were assessed for free growing status using published stocking standards. In the SBSdw3, 50 of 130 plots (38.5%) were free growing, for the SBSdk, 65/130 plots (50%) were free growing, and in the SBSmc, 73 of 130 plots (56.2%) were free growing. Figure 7 shows a distribution of the number of plots per site that were free growing, by subzone, for sites where 5 plots were measured (20 sites per subzone). No trends by subzone were apparent from these results.

3.4 Mortality Dates, Height, and Radial Growth

In most sampled stands, trees were killed by mountain pine beetle over several years, although in most stands there was a single year that dominated in terms of number of trees killed (the mode of mortality dates). Mortality dates by subzone are shown in Figure 8. In the SBSdk, 1999 was the peak year of mortality, with a smaller peak in 2002. In comparison, the SBSdw3 stands experienced mortality consistently across years 2003, 2004, and 2005. The SBSmc stands had mortality peaks separated by about three years, starting with 1998, then 2002, and 2005.

Mean height growth over one-year and five-year periods for seedlings and saplings was greater for saplings of all species compared to seedlings, and no consistent difference among species was observed (Figure 9). Analysis of variance of one-year vertical growth for seedlings and saplings combined among different species by sites showed no significant differences in the SBSmc3 ($p = 0.348$), SBSdw3 ($p = 0.235$), and the SBSdk ($p = 0.095$). In the SBSmc2 however, subalpine fir showed greater height growth over the past year than other species ($p = 0.008$). Analysis of variance of height growth over the past five years showed no significant differences among species within the SBSdw3. In the SBSdk, subalpine fir had significantly lower growth than the other species ($p = 0.028$), whereas in the SBSmc2, subalpine fir had greater growth ($p < 0.001$), and in the SBSmc3 pine had greater growth than subalpine fir and black spruce ($p = 0.003$).

Radial growth responses to overstorey mortality due to mountain pine beetle were evident in all understorey species sampled. Both interior spruce and black spruce showed a higher rate of radial growth release than pine and subalpine fir (sample size for Douglas-fir was too small to use in this comparison). Table 4 shows the number of trees showing release by species.

Table 2. Incidence in percent of biotic and abiotic agents for non-host specific or grouped agents observed in canopy trees (> 7.5cm dbh).

Agent	SBSdw3					SBSdk				SBSmc2				SBSmc3			
	Bl	Fd	Pl	Sb	Sx	Bl	Pl	Sb	Sx	Bl	Pl	Sb	Sx	Bl	Pl	Sb	Sx
Physical: Animal	16.3	8.2	2	0.8	5.1	0	2.8	2.5	7.2	0.7	4.5	0	2.5	4.3	2.5	5.6	4.6
Defoliation[1]	1.55	0	0.1	0	1.04	0	0	0	0	2.8	0	0	2.5	0	0.1	0	0.35
Root Disease[2]	10.08	.97	6.4	4	6.1	0	6	3.4	2.9	11.9	8.7	6.8	5	17.2	13.4	21.4	7.8
Cankers[3]	0.8	2.4	1	0	1.9	0	0.9	0	0.9	0	3.4	2.3	0	0	0.7	0.4	2.1
Bark Beetles	0	0.4	69.2	0	1.2	0	68.7	2.5	2.3	0	43.2	2.5	0	0	66.5	.7	2.5

(Note: Bl = subalpine fir, Fd = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

[1] Defoliation includes identified defoliator fungi (e.g. *Dothistroma*) and defoliation caused by unidentified agents.
[2] Root disease includes disease caused by *Inonotus tomentosus* and unknown agents.
[3] Cankers includes unidentified agents on all species and *Atropellis* on pine.

12
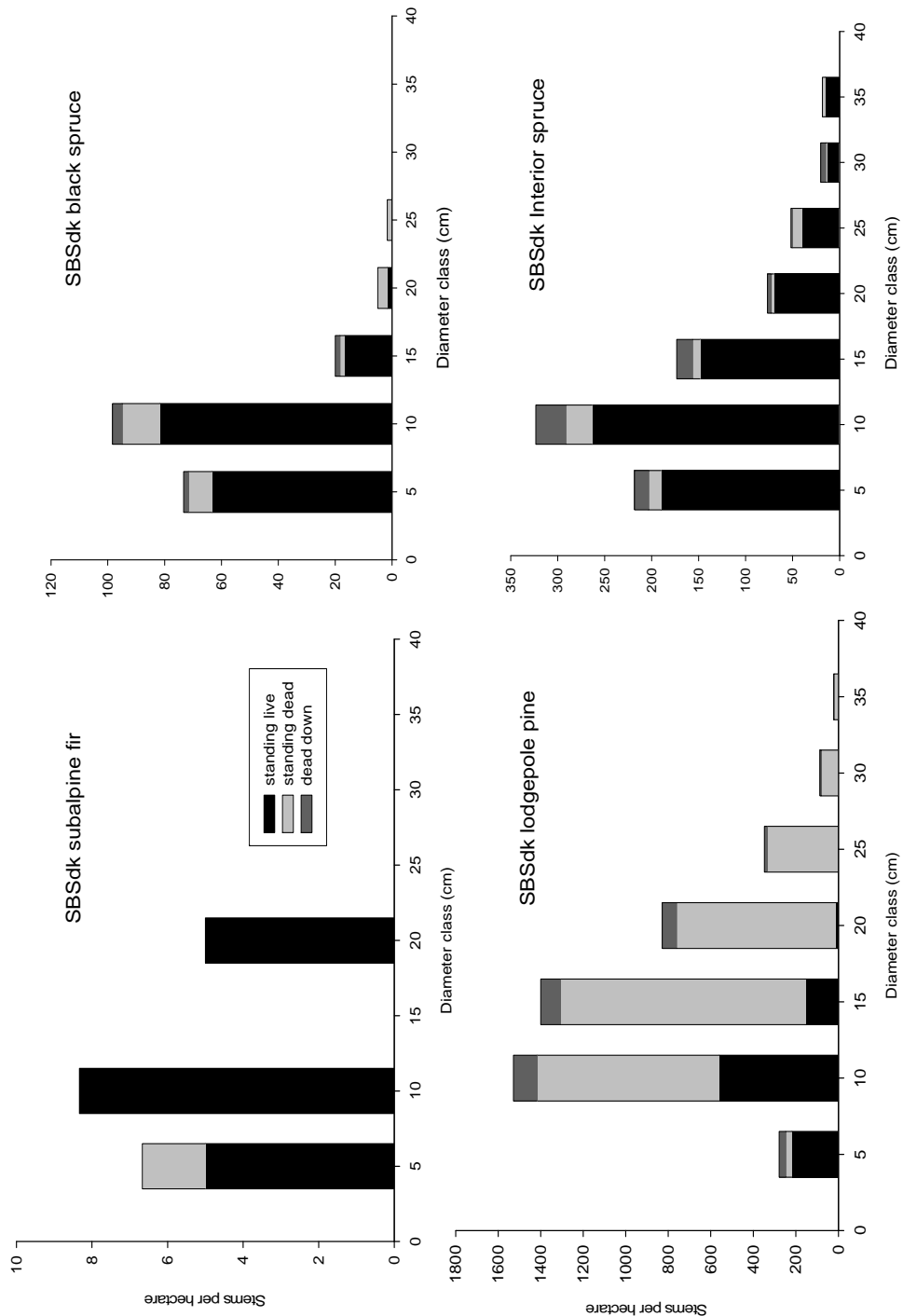
Figure 6a. Distribution of canopy trees by diameter class and condition for the SBSdk.
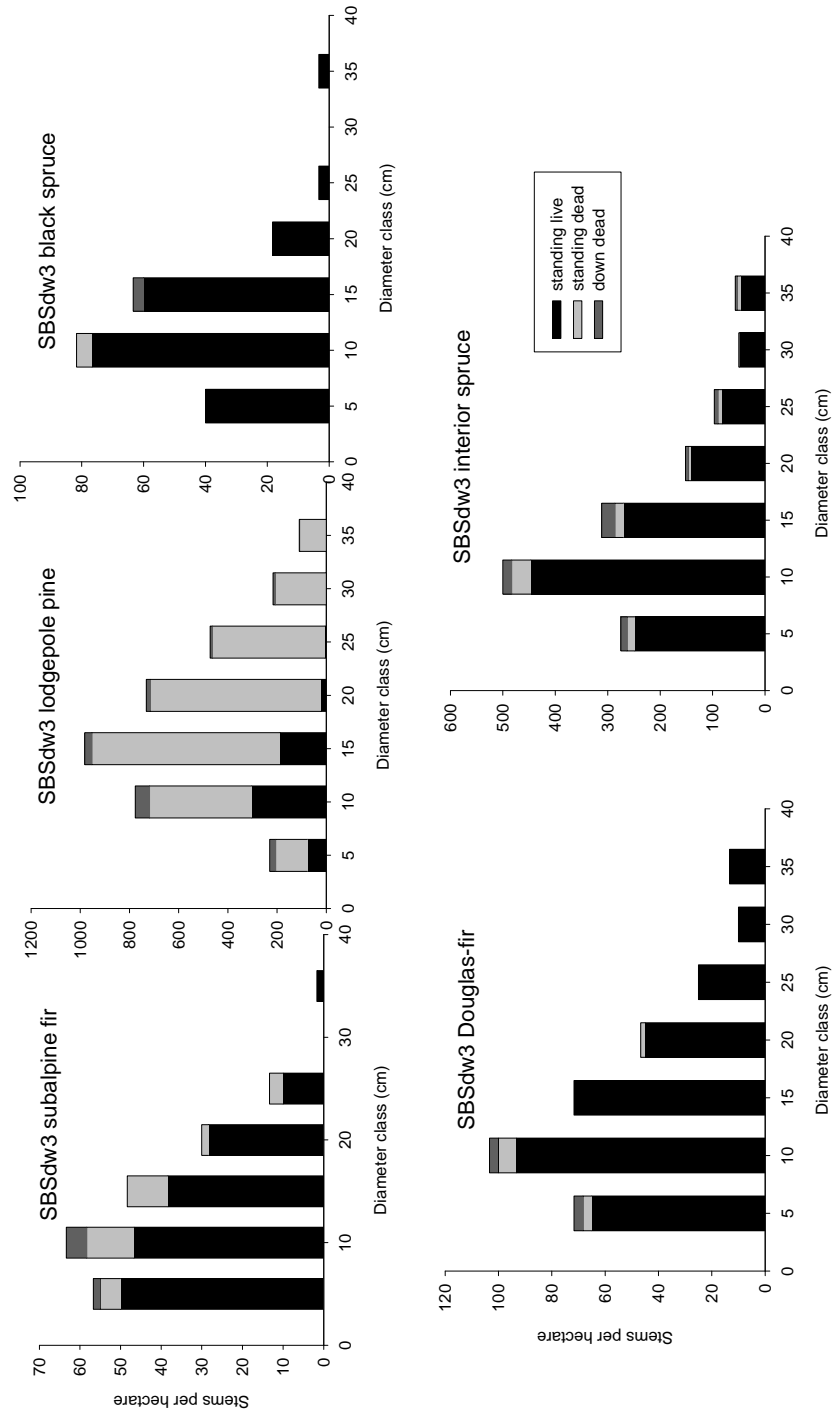
Figure 6b. Distribution of canopy trees by diameter class and condition for the SBSdw3.

14
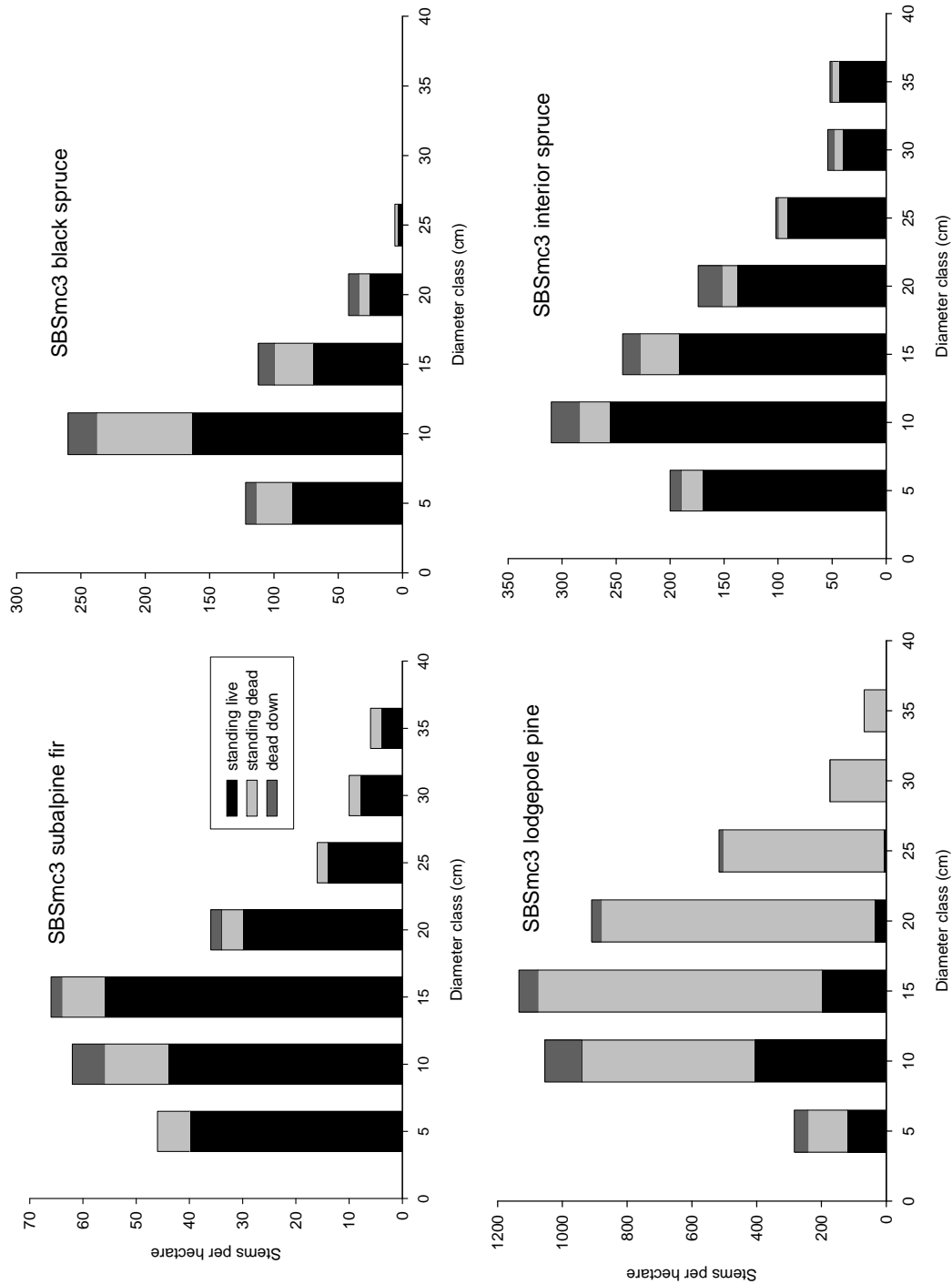
Figure 6c. Distribution of canopy trees by diameter class and condition for the SBSmc3.

15

Figure 6d. Distribution of canopy trees by diameter class and condition for the SBSmc2.
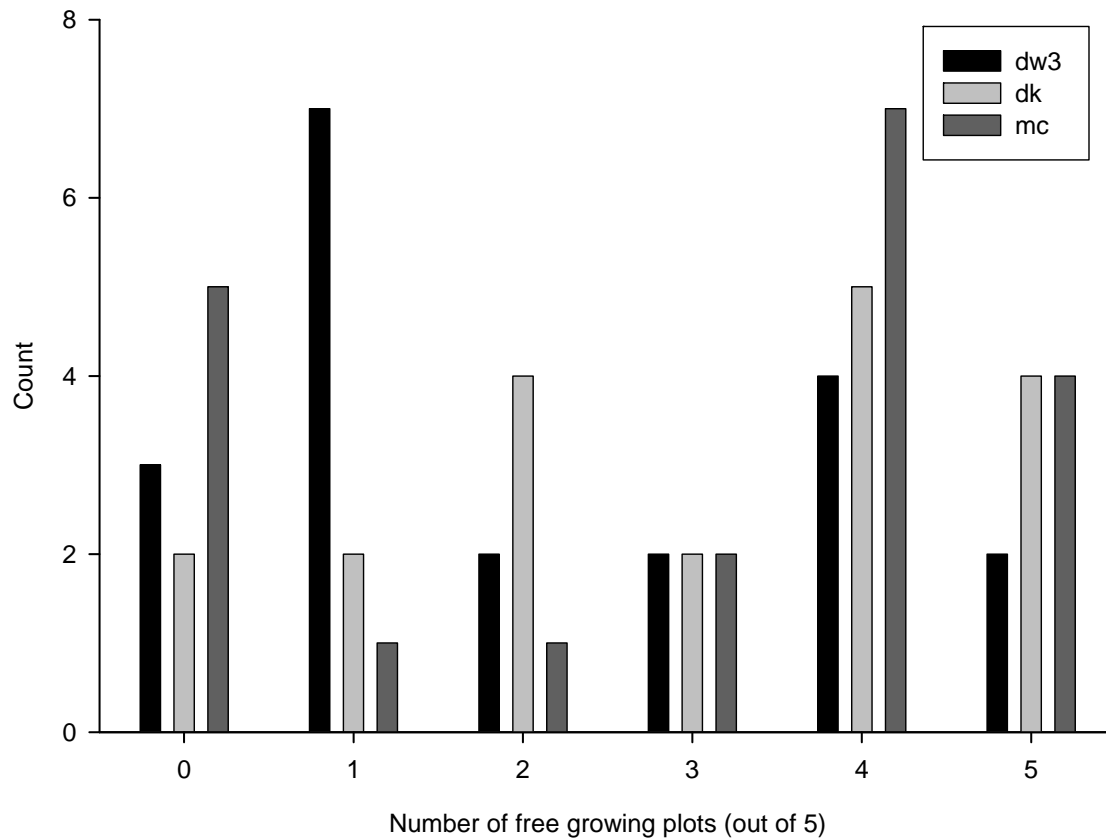
Figure 7. Number of free growing plots (out of 5 per stand) in three subzones: SBSdw3, SBSdk, and SBSmc.

Table 3. Incidence in percent of host specific biotic agents observed in canopy trees (> 7.5 cm dbh).

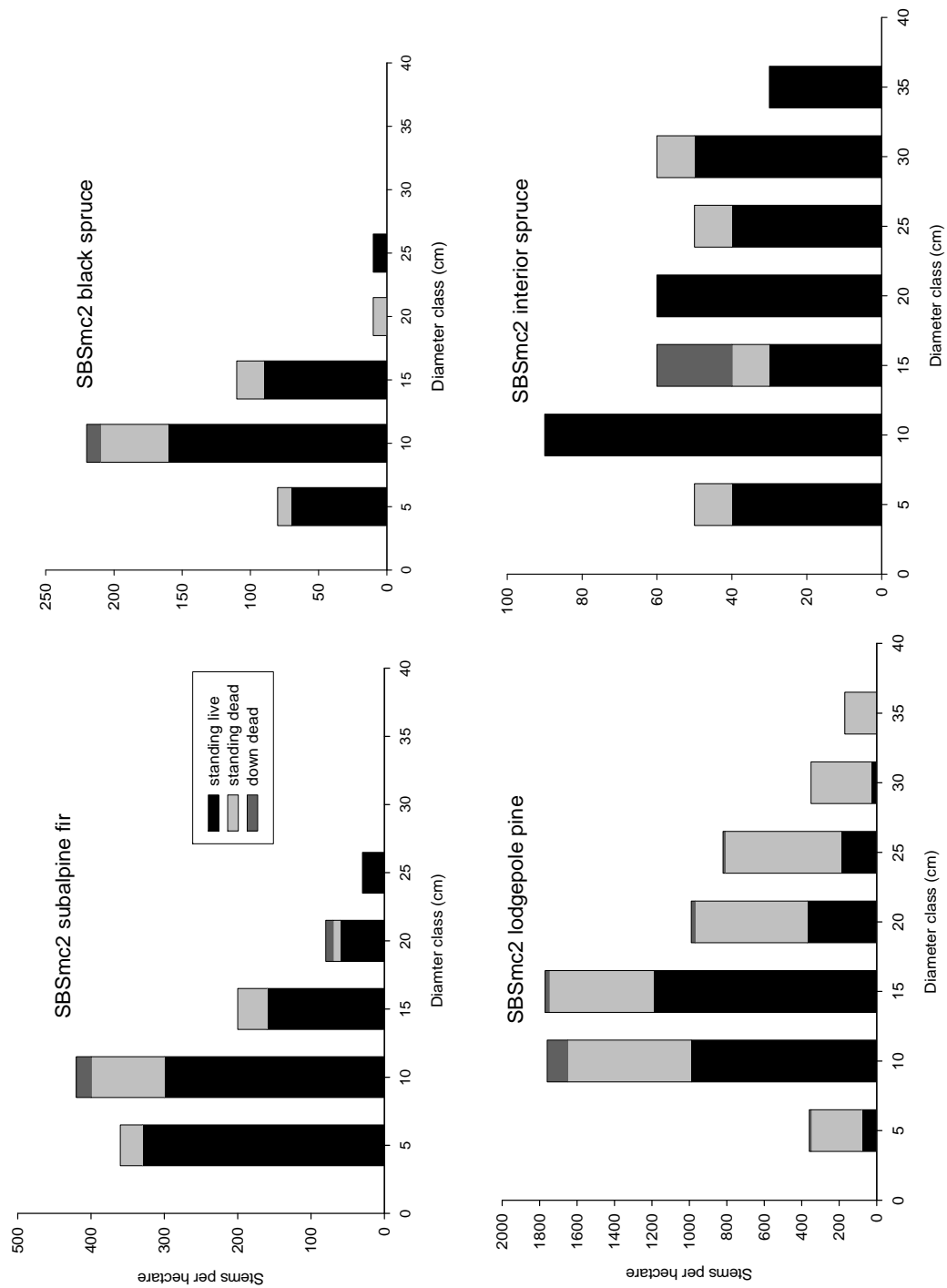| Agent	SBSdw3	SBSdk	SBSmc2	SBSmc3
Fir broom rust	3.1	16.7	0	4.3
Spruce broom rust	3.0	2.6	3.6	4.2
Western gall rust	0.7	0.5	1.29	0.3
Stalactiform blister rust	0	0.2	0.9	0.2
Dwarf mistletoe	0	0.9	0	0
Spruce gall adelgid	21.4	10.2	0	3.5
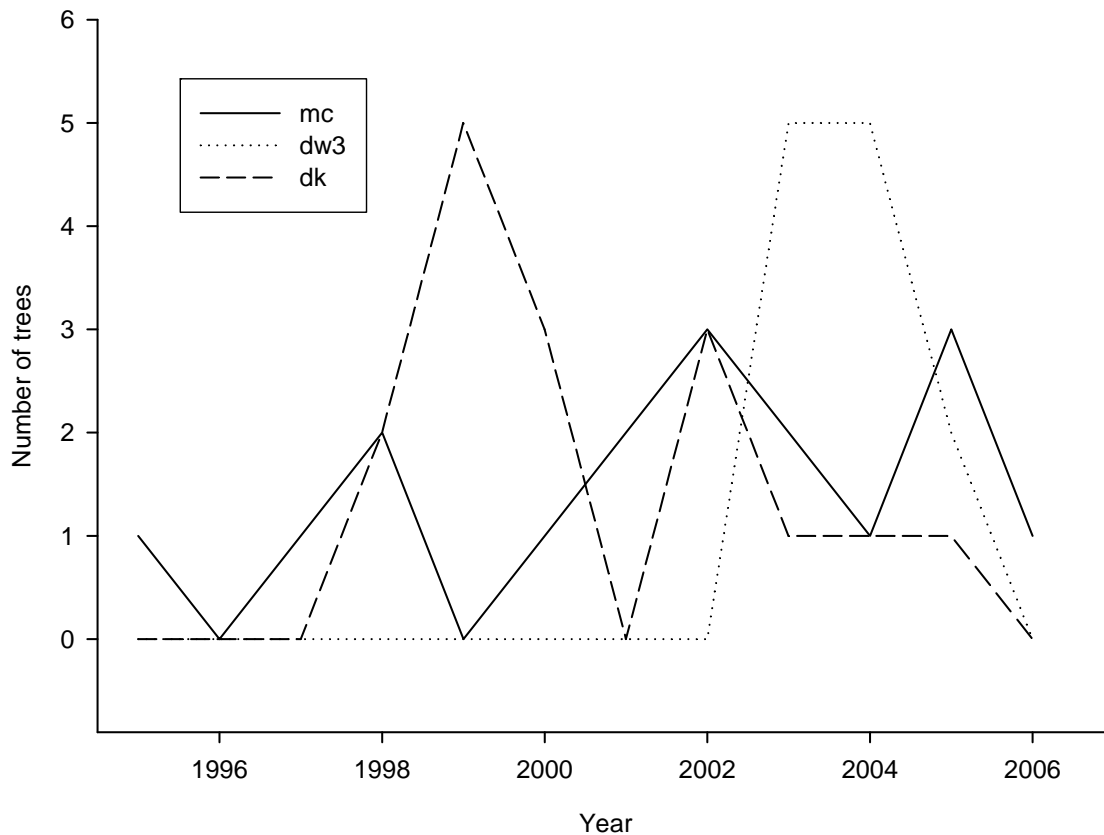
Figure 8. Number of mortalities of lodgepole pine due to mountain pine beetle per year by subzones.

Table 4. Number of crop trees sampled, number of growth releases recorded, and mean and range of growth releases per sample tree.

Species	Number of trees	Number of releases	Mean releases per tree	Range of releases per tree
Subalpine fir	29	45	1. 5	0–4
Douglas-fir	2	1	.5	0–1
Lodgepole pine	58	87	1.5	0–4
Black spruce	24	41	1.7	0–5
Interior spruce	60	117	1.95	0–6

Some of the sampled crop trees were sub-dominant in the canopy, which would not be expected to show a significant response to overstorey mortality. However, tree age did not have a significant effect on the probability of a crop tree releasing in response to the mortality caused by the most recent mountain pine beetle outbreak.
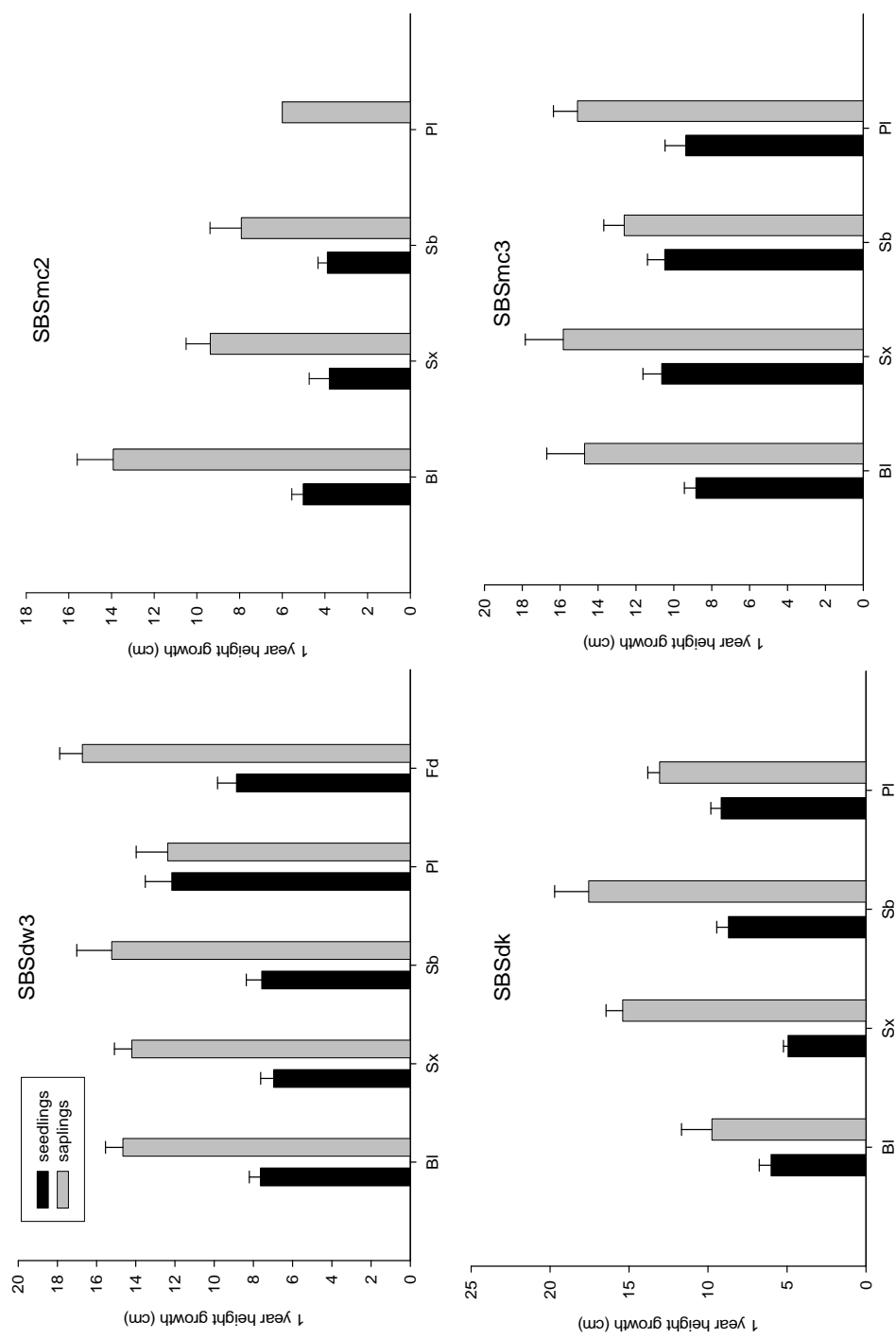
Figure 9a. Mean one-year height growth of advanced regeneration by subzone and species.
(Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

19
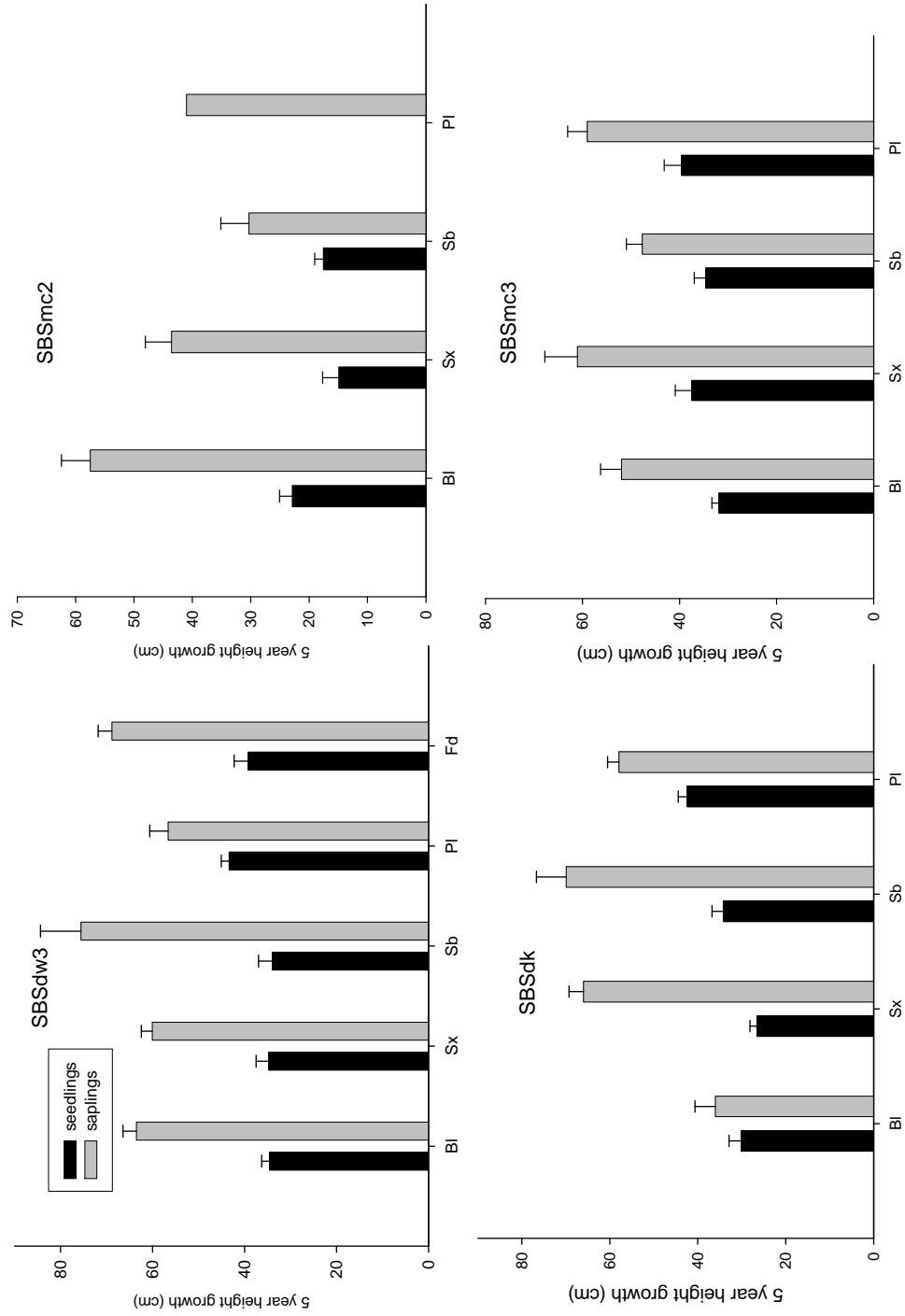
Figure 9b. Mean five-year height growth of advanced regeneration by subzone and species. (Note: Bl = subalpine fir, Sx = interior spruce, Sb = black spruce, Pl = lodgepole pine, Fd = Douglas-fir)

Figure 10 shows examples of the number of trees recording a growth release in three stands, one in each subzone. The SBSdk and SBSmc3 stands had trees that showed at least one growth release prior to the current outbreak, and then a very strong response to mortality caused by the current outbreak. Growth responses occurred within three years of the main mortality year. These stands were dominated by lodgepole pine and some spruce in the understorey. The SBSdw3 stand did not show the same sudden response to mortality, which in that stand was primarily in 2004.

The percent of trees recording a radial growth release following the main year of mortality in the stand is shown in Figure 11 for each subzone. In the SBSdk and SBSmc, most trees responded to the first peak in overstorey mortality, then the percent trees showing a growth release declined with increasing year of mortality. In the SBSdw3, fewer understorey trees responded to overstorey mortality, and all of the releases were clumped in the same period as the mortality occurred (2003–2005).

4. Discussion

Overall, the health of advanced regeneration in the stands that we studied was very good. The main damage agents were abiotic (e.g., deformities such as sweep) or resulted from animal browsing and rubbing. There were few biotic agents on the advanced regeneration that currently have the potential to cause significant damage. Agents such as defoliating fungi and insects, whose populations are highly regulated by environmental factors, have the most potential to become emerging pests due to climate change (Andrews 1992). The main drivers behind emergence of native pathogens include changes in cultural practices and weather (Anderson et al. 2004). Little is known about native emerging diseases, largely because they were historically thought to be benign and therefore did not attract much attention. Under the influence of climate change, emerging native pests may become more common and more devastating. Insects and pathogens dependent on specific weather conditions for infection and reproductive success (e.g., foliar pathogens and rust fungi) may be most susceptible to changes in climate. As emerging pests, their impacts may not be as sudden as those caused by introduced pests because of the relatively slow rate of change in the environment to more suitable conditions for emerging pests, compared to the sudden introduction of a new pest into a suitable environment. In this study, we found a few foliar diseases (dothistroma needle blight, red flag disease, and pine needle cast) that have the potential to increase in significance with climate change. Pathogens that cause foliar diseases are found in an environment of abundant substrate (foliage on conifer needles) with low levels of competition. They tend to have short life cycles and produce numerous offspring (spores) (e.g., *Dothistroma septosporum*; Gibson, 1972). At this point in time however, the incidence of foliar pathogens is quite low.

The second source of potential problems is pests that cause damage to mature trees and affect young trees as they grow. We identified two disease agents that have this potential. One was tomentosus root disease (caused by *Inonotus tomentosus*) and the second was lodgepole pine dwarf mistletoe. Tomentosus root disease affects spruce primarily, although it does occur regularly in lodgepole pine (Henigman et al. 1999). The causal agent spreads from root to root across root contacts and through infection by basidiospores (Gibson and Lewis 2004). Research has shown that there is not a significant increase in disease incidence following harvest—through increase in inoculum in cut stumps (Newbery et al. 2007). This suggests that sites with a significant amount of root disease could have a higher harvest priority, particularly if less susceptible species (e.g., subalpine fir) are favoured following harvest—either through protection of advanced regeneration or planting.
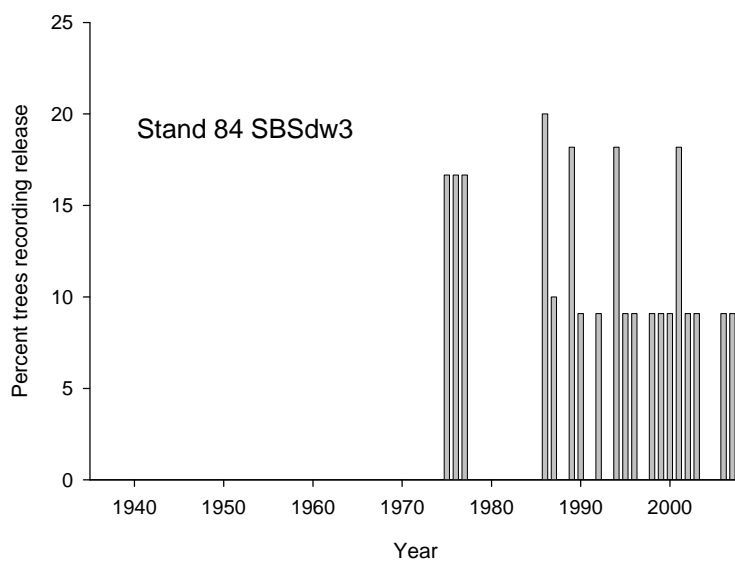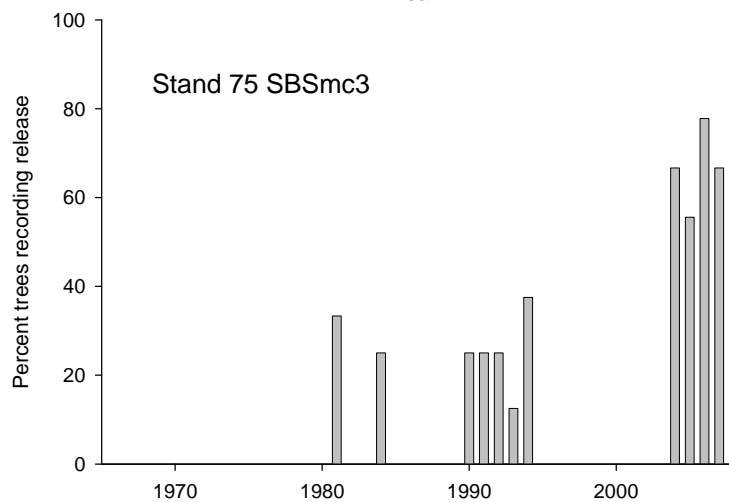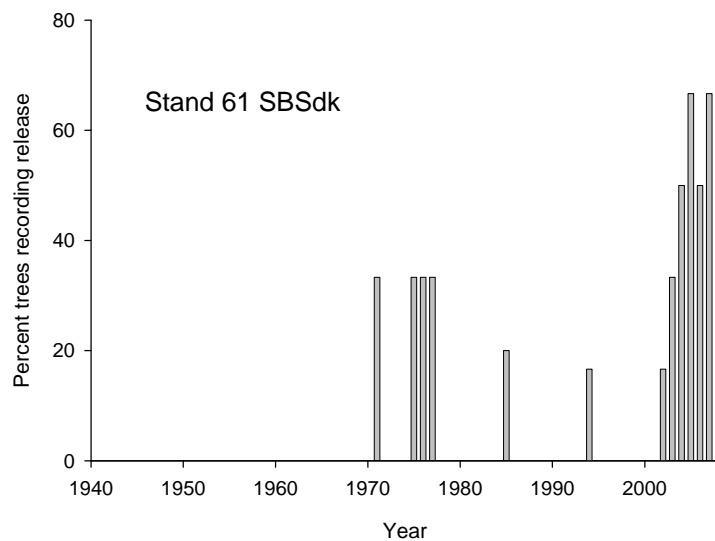
Figure 10. Percent trees recording release in each year for one stand in each subzone.
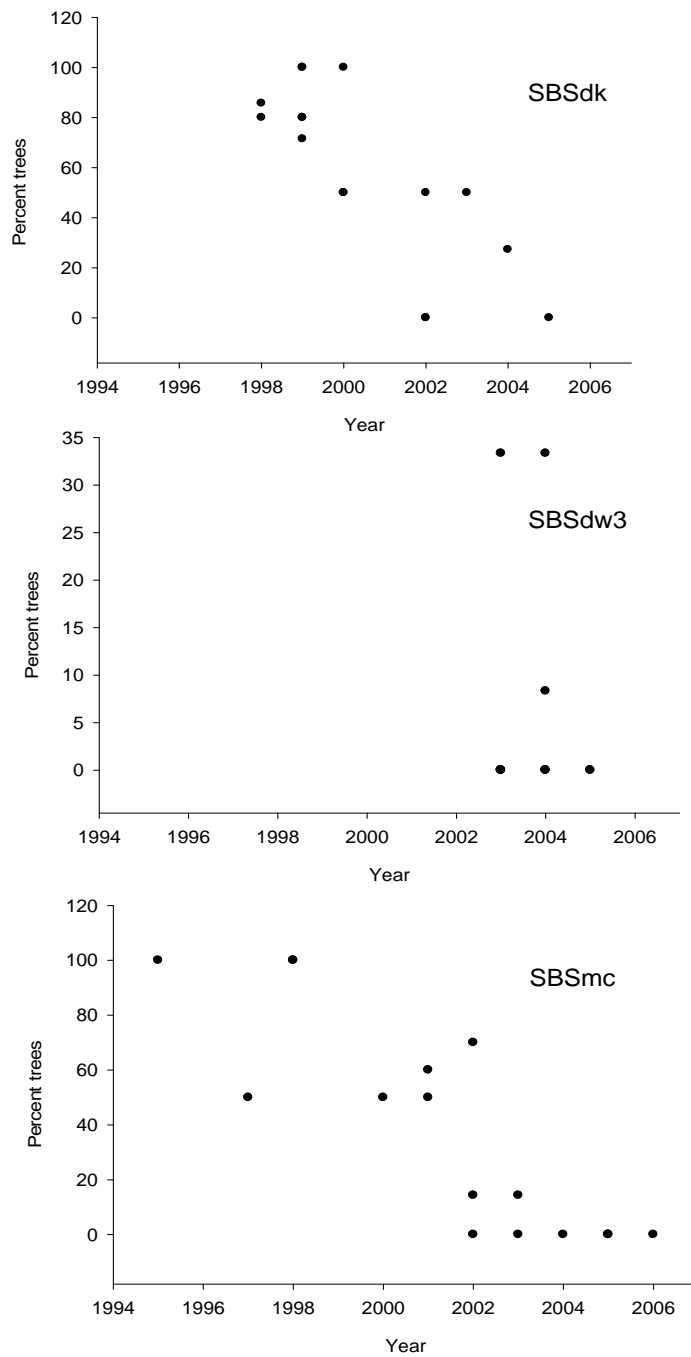
Figure 11. Percent trees showing a radial growth release following overstorey mortality in the same stand.

Similarly, sites with high levels of dwarf mistletoe in the overstorey, even if the overstorey is dead, will probably have high levels of infection in the pine understorey. On sites where pine is not the dominant advanced regeneration species, little infection is expected because dwarf mistletoe is host specific. Sites dominated by pine in the understorey, with significant amounts of dwarf mistletoe in the overstorey, could also have a higher priority for harvesting.

The limiting factor for satisfactory stocking by advanced regeneration is not the health of individual trees, but the species composition in the understorey. While subalpine fir did not dominate the understorey at any of the sites, it did form a significant proportion of the advanced regeneration. In some subzones and site series, plots were not sufficiently restocked according to the stocking standards because subalpine fir was not an acceptable species in that particular subzone and site series. It is expected that in both the SBSdw3 and SBSdk, where shade intolerant species such as Douglas-fir and lodgepole pine are present, that these species will benefit from the overstorey mortality, and may be able to obtain a position in the canopy and not be outcompeted by the shade tolerant subalpine fir.

Understorey trees showed strong and rapid release in response to overstorey mortality. Our study showed that trees in stands are attacked by beetles over several years. This observation was consistent with the findings of Lewis and Thompson (2009) who found trees in a stand were killed over a period up to five years, with the larger trees usually being attacked first. Growth releases occurred soon after the first significant attack year, usually within a year. Interior spruce appeared to have the strongest response to overstorey mortality, but growth releases were found in all tree species, and no significant differences were observed among species for radial growth response or vertical growth. Trees in SBSdw3 appeared to experience fewer growth releases (Figure 10) and were more likely to experience continual high growth, without a notable period of release in comparison to trees in the other two subzones. This lack of response by the SBSdw3 trees could be due to the low number of pine in these stands relative to the other sites. Larger growth release responses are expected in areas where there is a significant and sudden change in resource availability due to overstorey mortality.

5. Conclusion

Within the study area, trees in the understorey of stands that suffered significant mortality are very healthy and show strong radial growth responses to peak years of overstorey mortality. Most of the damage to potential crop trees is from abiotic causes, such as deformities from sweeps presumably due to snow press, and from browsing and other damage by mammals. Lodgepole pine is the most susceptible species to foliar diseases of all the species sampled, and because pine makes up a smaller component of the understorey, for the next rotation at least, the risk of foliar disease problems is fairly low. The lack of free-to-grow status in some of the plots was not due to pests or damage, but to the species composition of the understorey in that subalpine fir is not an accepted species in some of the study area.

6. Acknowledgements

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