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Influence of decay fungi on species composition and size class structure in mature *Picea glauca* × *engelmannii* and *Abies lasiocarpa* in sub-boreal forests of central British Columbia

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Abstract

Disturbance patterns in the sub-boreal spruce forests of central British Columbia have long been thought to result from frequent stand-initiating fires. However, recent evidence suggests that fires in the wetter areas of this region are infrequent (>500 years) and the uneven-aged stand structures have been shown to be self-maintaining in the absence of fire. The importance of decay fungi as agents of gap-formation and facilitators of uneven-aged stand structure was investigated. Three plots on each of two recently clearcut sites were established. Each stump in the plots was stem mapped and the species and diameter recorded. Decay at the stump top was recorded as white or brown rot, and the area occupied by decay was measured. Spruce stumps dominated the larger diameter classes but had less butt rot than sub-alpine fir stumps. Decay fungi contribute to stem breakage in living trees with heart rot, and as saprots of dead trees. Therefore, the results suggest that decay fungi play an important role in removing sub-alpine fir trees from the canopy of these wetter sub-boreal ecosystems, and in enabling spruce recruitment. The type of decay observed in sub-alpine fir suggests that breakage is predominantly due to white rot fungi causing heart rot, such as *Echinodontium tinctorium* and *Stereum sanguinolentum*. In spruce, brown rot fungi, which are predominantly saprot or wound-entry decay fungi, became more common in larger spruce, and may result from wounding as sub-alpine fir fall from the canopy. Spatial analysis indicated the stumps with stem decay were clumped. However, this is more likely due to strong clumping of the host, rather than spreading of butt rot pathogens through the roots.

Keywords: Canopy gap; *Echinodontium tinctorium*; Decay; Disturbance; Sub-boreal

1. Introduction

Forests of central British Columbia range from dry lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), ponderosa pine (*Pinus ponderosa* Laws.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands, to wet-forest types dominated by a hybrid spruce (*Picea glauca* × *engelmannii*) and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The drier forest types are primarily even-aged stands that result from stand establishment following fire. The impact of fire as a stand-replacing disturbance agent decreases along

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a gradient from west to east, as elevation and precipitation increases due to the effect of the Rocky Mountains (Ministry of Forests, 1995).

The part of the central interior near Prince George, B.C., has been described by Meidinger and Pojar (1991) as the sub-boreal spruce (SBS) zone. According to the B.C. Ministry of Forests, stand-initiating fire return intervals for this zone range from 100 to 200 years (Ministry of Forests, 1995). However, recent work by Hawkes et al. (1997) strongly suggests that, in wetter ecosystems of this zone, fire return intervals commonly reach 500 years and up to 1000 years in some areas. Lindgren and Lewis (1997) sampled ages of spruce and sub-alpine fir trees in an area 65 km northeast of Prince George and found the oldest trees were between 200 and 330 years. Hawkes' work, based on historical patch sizes and shapes, and fire records, indicates that stand ages are much greater than the oldest trees within the stands. Oliver and Larson (1996) describe this as a true old-growth stage where all trees regenerating after a stand-replacing event have themselves been replaced. This suggests that, between stand-initiating events, there are processes occurring on a smaller scale which shape the age class structure and species composition of these wet sub-boreal ecosystems. Such process are characterized by single or small-group tree fall gaps, and have been well documented in several related forest types including the central Rockies (Aplet et al., 1988; Veblen, 1986), the southeastern boreal forest (Kneeshaw and Bergeron, 1988), and northwest central B.C. (Kneeshaw and Burton, 1997).

Insects and fungi are the primary biotic agents of single tree or small group disturbances that occur commonly in the central interior of B.C. The spruce beetle (*Dendroctonus rufipennis* Kirby) is the most significant insect pest of North American spruce forests (Furniss and Carolin, 1980). During periods of outbreak, this insect can cause up to 90% mortality of spruce trees (Humphreys and Safranyik, 1993). In uneven-aged stands, this leads to death of large diameter spruce trees, while smaller and non-host trees remain unattacked (Lindgren and Lewis, 1997). Tomentosus root disease of spruce, caused by *Inonotus tomentosus*, spreads both by root contacts and by spore infections (Lewis and Hansen, 1992, 1991) and results in small groups of dead or dying spruce trees. The fungus is ubiquitous to the boreal and sub-boreal forest (Basham and Morawski, 1964; Davidson and Redmond, 1957; Hobbs and Partridge, 1979; Patton and Myren, 1968; Whitney, 1962). In central B.C., it is found more commonly in mesic and submesic sites (Bernier and Lewis, 1999). Sub-alpine fir appears to be resistant to infection by *I. tomentosus* (Whitney, 1980, and personal observations), but is highly susceptible to *Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh., one of the most common fungi found throughout the central interior of B.C. This is a heart rot fungus which enters the trees through small twig stubs, and over several decades can result in an extensive column of decay in the tree's heartwood (Etheridge and Craig, 1976). There are many other fungi that can cause decay of living conifers in this area. Waldie (1949) compiled a list of 19 identified fungi isolated from the root and butt sections of living spruce in the upper Fraser region. Within the same region Bier et al. (1948) studied decay in subalpine fir. They isolated and identified numerous decay fungi, with *S. sanguinolentum* and *Echinodontium tinctorium* accounting for >87% of the volume of decay in living trees.

In mature forests of central B.C., interior hybrid spruce dominates the canopy layer, but the understory layer and the smaller size classes of the overstory layer are composed primarily of sub-alpine fir (Kneeshaw and Burton, 1997). Given the greater apparent recruitment of sub-alpine fir to the understory, and its shade tolerance, one would expect to find many stands dominated by sub-alpine fir following an outbreak of spruce beetle or in areas with a high incidence of tomentosus root disease. However, Lindgren and Lewis (1997) and Veblen (1986) found that in central B.C. and the Colorado front range, respectively, spruce continues to dominate the canopy. Veblen (1986) concluded that this was due to species specific mortality of sub-alpine fir. Furthermore, Kneeshaw and Burton (1997) found that *Abies* recruitment occurs continuously throughout stand history, whereas spruce recruitment is sporadic. Single-tree disturbances were found to be important at accelerating *Picea* initiation into the understory. They concluded that these spruce-fir stands can be self-perpetuating in the absence of fire.

The purpose of this study was to quantify the incidence of butt rot in spruce and sub-alpine fir stands in wet ecosystems of the SBS zone, and relate that incidence to the distribution of tree sizes by species. The objectives were to:

1. determine the size class distributions of spruce and sub-alpine fir in a wet ecosystem of the SBS zone;
2. determine the incidence of butt rot by size class;
3. relate decay incidence to species recruitment in the understory and species ascension to the overstory; and
4. examine the spatial relationship between decayed trees and healthy trees.

2. Materials and methods

Sampling was carried out on stumps in recent clearcuts to facilitate identification and quantification of internal decay in trees. Two recently cut stands in the very wet, cool ecosystem of the SBS zone (Meidinger and Pojar, 1991) were located in an area ≈65 km northeast of Prince George at an elevation of ≈750 m. The climate of this zone is continental, with seasonal extremes of temperature. Mean annual temperature ranges from 1.7° to 5°C, and mean annual precipitation ranges from 440 to 900 mm, of which 25–50% is snow (Meidinger and Pojar, 1991). The stands were uneven aged according to age measurements taken on trees in a neighboring stand (Fig. 1).

In each stand, three plots were located on a transect line that ran through the middle of the long axis of the clearcut. The plots were located 200 m apart and were $50 \times 50\ m^2$ in size. Each stump, including those of apparently dead trees at the time of harvest, was stem-mapped using a Nikkon Total Station, and the tree species, stump diameter, type of decay (brown or white rot) and diameter of decay at the stump top were recorded.

Stumps were placed into 10-cm diameter categories as follows: Diameter Class 1 = 10–19 cm, Class 2 = 20–29 cm, Class 3 = 30–39 cm, Class 4 = 40–49 cm, Class 5 = 50–59 cm, Class 6 = 60–69 cm, Class 7 = 70–79 cm, and Class 8 = 80+ cm. The number of stumps in each category by species was determined for each site. The percentage of stumps with butt rot was calculated for each diameter category at each site. Where appropriate, the percentage of colonized stumps was regressed on stump diameter class for each species to describe the relationship between tree size and incidence of decay. To analyze the severity of butt rot by diameter class, the percent area at the stump top occupied by decay was calculated for all colonized stumps in each diameter class, and for all stumps in each diameter class.

The distribution of stump-diameter data was compared across both sites by species using a Kolmogorov–Smirnov two-sample test (Sokal and Rohlf, 1995) to determine if data from the sites could be

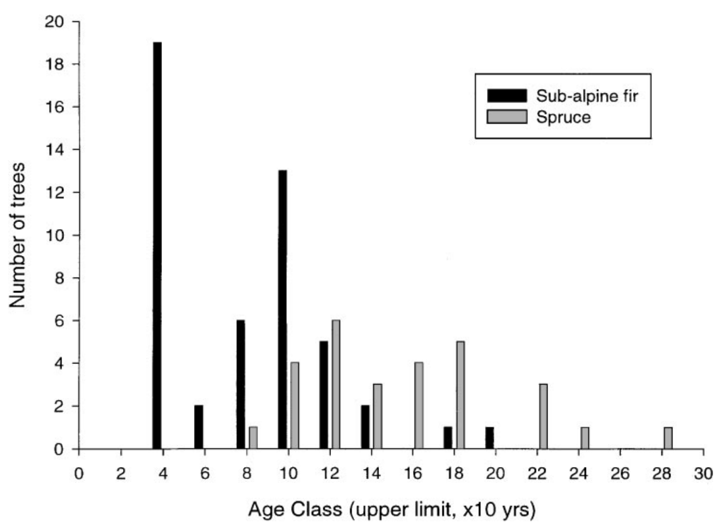

Fig. 1. Age-class distribution for spruce and sub-alpine fir trees in a stand neighboring the study site.

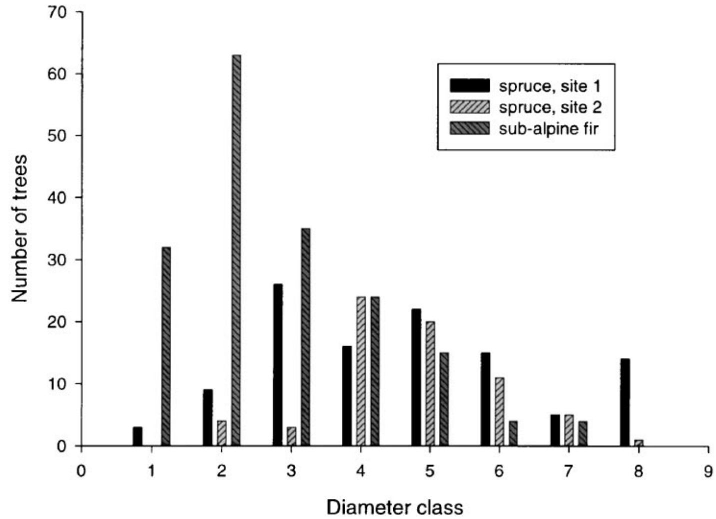

Fig. 2. Frequency distributions of spruce and sub-alpine fir trees by diameter class.

combined. Graphs of frequency by diameter class, and percent stumps with butt rot by diameter class were prepared.

Stem maps of each plot were prepared and each stump was coded by species and the presence or absence of butt rot. These maps were examined for evidence of clumping of trees with butt rot using methods similar to those of Van der Kamp (1995). For all data combined, two sizes of grid were overlaid on the stem maps and the number of trees by species, and the number of trees with butt rot, were counted in each square. The grid sizes were $10 \times 10\ m^2$ and $20 \times 20\ m^2$. Variance to mean ratios for each species, and the number of stumps with butt rot, were calculated at each grid size. Ratios significantly >1 indicated a clumped distribution. Expected frequencies for each species, and the number of infected trees, were calculated using the mean value and a Poisson distribution. Expected and observed frequencies were compared by a χ^2 test. All statistical tests were carried out using SPSS Systat 6.0.

3. Results

The Kolmogorov–Smirnov two-sample test indicated that diameter distributions for the two sites were not significantly different for sub-alpine fir ($p = 0.957$) but were significantly different ($p = 0.04$) for spruce. Other work on spruce in similar ecosystems (Kneeshaw and Burton, 1997, Newbery[1] – unpublished data) has shown that the age and diameter class distribution of spruce in different stands is highly variable. Therefore, only the sub-alpine fir data were combined for analysis of decay incidence. Fig. 2 shows the diameter class distributions for spruce and sub-alpine fir. Sub-alpine fir has more stems in the smaller diameter classes (<30 cm DBH), and spruce has more stems in the 30–60 cm DBH range.

The incidence of butt rot increases with diameter class for sub-alpine fir (Fig. 3) and the relationship is linear ($p = 0.001$, $R^2 = 0.917$). For spruce, the incidence of decay at Site 2 was highest in trees of 50–59 cm diameter; Site 1 showed a more even distribution of percent trees with butt rot (Fig. 3). The percent spruce trees with butt rot on both sites fit a Weibull distribution according to Kolmogorov–Smirnov tests ($p < 0.001$, both the sites). Although spruce had a lower incidence of decay than sub-alpine fir at diameters >40 cm, for those trees that did have butt rot, the percent surface area occupied by decay was greatest for spruce over most diameter classes (Fig. 4).

The type of decay also varied between the two species, and by diameter class (Fig. 5). White rots are caused by fungi that degrade lignin and cellulose. Brown rot is caused by fungi that are very efficient

[1]Ted Newbery, University of Northern British Columbia, Prince George, B.C.

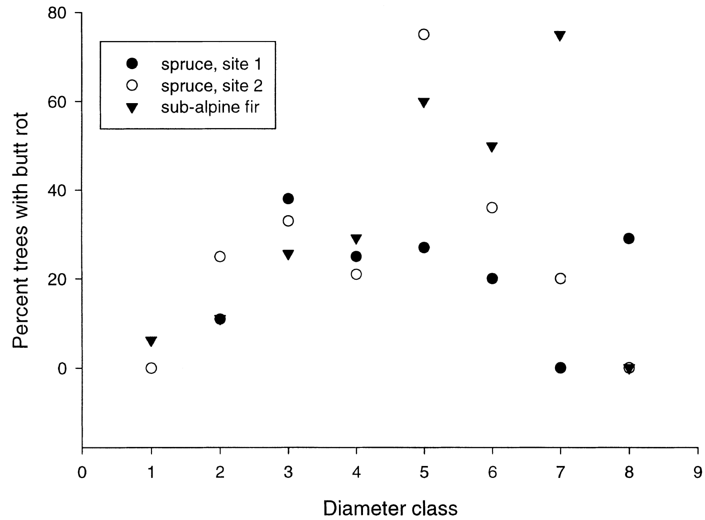

Fig. 3. Percent of spruce and sub-alpine fir trees with butt rot by diameter class.

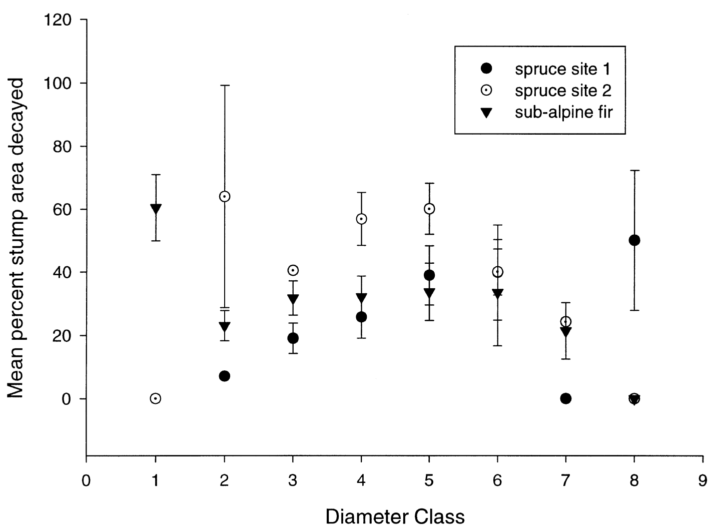

Fig. 4. Percent of stump area at the stump top occupied by butt rot by diameter class for spruce and sub-alpine fir.

metabolizers of cellulose, but do not degrade lignin (Callan and Funk, 1994). White rot was dominant in sub-alpine fir stumps across all but one age class. Brown rot was found only in stumps from 30 to 59 cm diameter. In spruce, incidence of white rot was similar to brown rot in small diameter classes, but in larger diameter stumps (50+ cm), brown rot dominated.

Variance to mean ratios of each species and decayed stumps by grid squares in two different grid sizes are given in Table 1. Variance to mean ratios are all >1, indicating that the distributions of both, the trees and butt rot are clumped rather than randomly distributed. χ^2 comparisons of observed frequencies against expected frequencies constructed using a Poisson distribution show that the spatial distributions of both, the trees and butt cull are significantly different from random at the 10-m grid size. At 20-m grid size, only the distributions of spruce and spruce with rot are significantly different from random (Table 1).

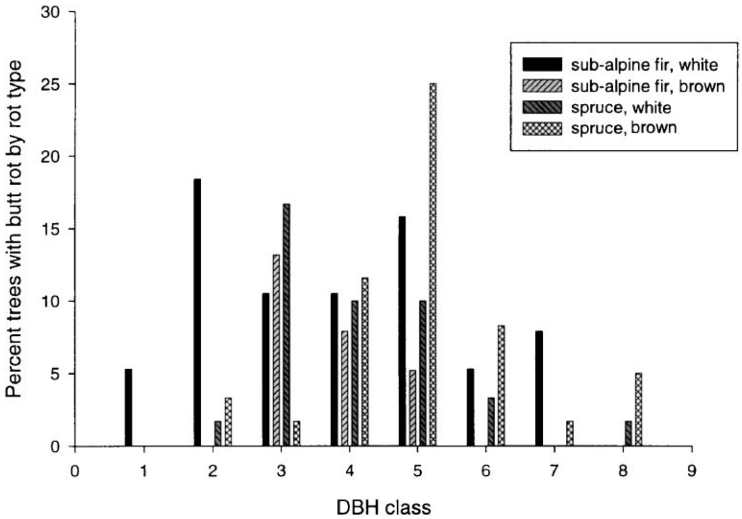

Fig. 5. Distribution of white and brown rot in spruce and sub-alpine fir trees by diameter class.

Table 1
Variance to mean ratios, and p values from χ^2 tests of observed vs. expected frequencies in grid squares of two different sizes

	10 m grid size					20 m grid size				
	fir with rot	total fir	spruce with rot	total spruce	total with rot	fir with rot	total fir	spruce with rot	total spruce	total with rot
V (m)	1.3	1.63	1.27	1.61	1.43	1.26	2.2	1.48	1.81	1.46
p	0.02	0.035	<0.001	<0.001	<0.001	0.77	0.25	<0.001	<0.001	0.0759

4. Discussion

In the wetter ecosystems of the sub-boreal spruce zone (SBS), fire return intervals are less frequent than was previously thought (Hawkes et al., 1997; Jull, 1997). The period between stand-initiating events is a time of slow conifer establishment (Kneeshaw and Burton, 1997), followed by recruitment of trees to the canopy as other individuals or small groups of trees are killed. Kneeshaw and Burton (1997) demonstrated that in the moist, cool subzone of the SBS, sub-alpine fir dominated the understory, but was proportionately less frequently recruited to the canopy. The observations made in this study, of dominance by spruce in larger diameter classes and older age classes, coupled with increasing butt rot in fir as diameter increases, is consistent with the findings of Kneeshaw and Burton (1997). The distribution of butt rot frequency by diameter class in sub-alpine fir suggests that root and stem rots may be an important factor in limiting the number of fir in the overstory. Worrall and Harrington (1988) identified root and butt rots as the most important group of biotic diseases at all elevations of spruce-fir forests studied in New Hampshire. The primary effect of root and butt rot was to predispose trees to breakage near ground level. Their gap-development study identified large spruce as the primary gap-makers. They suggested that, especially on lower slopes, balsam fir was a less important stand component due to its high susceptibility to root pathogens.

Aplet et al. (1988) described the phases of spruce-fir stand development in the Colorado Rockies. According to their chronosequence, after a major disturbance and following a period of recolonization by both, spruce and sub-alpine fir, spruce goes through an exclusion phase that is not shared by sub-alpine fir. This is followed by a spruce re-initiation phase that is associated with high mortality in the overstory. During this phase, the number of sub-alpine fir in the oldest age classes is reduced and the basal area of sub-alpine fir decreases by half. In the Colorado Rockies, this occurs at ca. 300 years following stand initiation. Veblen's study of Engelmann spruce and sub-alpine fir also found that the abundance of sub-alpine fir was much greater than that of spruce in size classes of <8 cm. At >40 cm DBH, the reverse was true. He also found that sub-alpine fir accounted for 75% of all tree falls. Furthermore, windsnap accounted for 69.7% of those treefalls, indicating that the trees were decayed and/or dead before they fell. In further support of a strong correlation between decay and mortality due to breakage, Hennon (1995) observed high levels of heart rot in western hemlock/Sitka spruce stands of coastal Alaska with many large trees dying from bole breakage. Stands in earlier stages of development lacked both high levels of heartrot and bole breakage.

The role of decay fungi, in particular *Echinodontium tinctorium*, in removing *Abies* from the overstory and providing nurse logs for the regeneration of spruce (Fowells, 1965) may be substantial in these ecosystems. To describe quantitatively the impact of decay on wood volume yield, Meinecke (1916) defined the term 'pathological rotation age' to mean the age of a stand when decay losses exceed mean annual increment. This age can vary widely according to species and region. Several studies on decay of *Abies balsamea* (L.) Mill. in Ontario suggest a pathological rotation age for balsam fir of 70 to 80 years (Basham, 1991). Bier et al. (1948) found a higher pathological rotation age of 130 years for sub-alpine fir in central B.C. Spruce in central B.C. is more resistant to stem decay than sub-alpine fir, and has a pathological rotation age of 150 to 175 years (Etheridge, 1958).

Altogether, these studies indicate that bole breakage is an important, and often overlooked, cause of mortality, and that decay contributes significantly to bole breakage. Therefore, it follows that the higher incidence of decay in sub-alpine fir relative to spruce, in trees >50 cm diameter, is a significant contributor to higher rates of treefall by sub-alpine fir.

The type of decay found most commonly in the two species is also important with respect to stages of decay development and contribution to treefalls. The dominance of white rot fungi in sub-alpine fir in this study suggests that most of the trees were infected by either *E. tinctorium* or *S. sanguinolentum*, as they are the most common sub-alpine fir fungi in this area (Bier et al., 1948). Both of these fungi can cause extensive decay columns which is an important factor in the likelihood of bole breakage.

Echinodontium tinctorium is a true heart rot that enters the tree through shade-killed branchlets, ca. 1 mm in diameter (Etheridge and Craig, 1976). Trees are ca. 40 years old before the branchlet stubs have developed to the stage where they can serve as infection courts. Infections can become dormant for many years and development of decay may be activated by conditions associated with large branch stubs or deep injuries (Etheridge and Craig, 1976). This may explain the observed monotonic increase of butt rot incidence with increasing diameter class, as larger trees are more susceptible to attack and decay development (Wilson, 1997). This also suggests that the white rot observed in the smaller diameter classes is predominantly caused by *S. sanguinolentum*. This is a saprot fungus that Bier et al. (1948) found commonly associated with a variety of wounds, such as frost cracks and root injuries (Etheridge, 1973), on sub-alpine fir in the central interior of BC. Given the demonstrated relationship between stem decay and mortality (Hennon, 1995; Veblen, 1986; Worrall and Harrington, 1988), it is suspected that the decrease in sub-alpine fir stems in larger diameter classes is closely associated with the increase in stem decay.

In spruce, white rot was more common in the smaller diameter classes and brown rot more common in the larger. White rot in spruce is generally attributed to *I. tomentosus*, *S. sanguinolentum*, *Corticium galactinum*, or *Phellinus pini* (Waldie, 1949, and personal observations). *Phellinus pini* causes a true heart rot that is more commonly observed in older trees due to a higher incidence of infection courts and more heartwood (Lewis, 1997a). *I. tomentosus* is a root rot that spreads by root contacts, and is more likely to infect larger trees because of larger root systems (Lewis, 1997b). Brown rot in spruce occurs as a result of wounds and attack by fungi that are normally saprophytic. The chance of wounding increases with tree age and, therefore, diameter and may explain why brown rots were more prevalent in the larger diameter classes than white rots. Overall decay incidence was highest in the middle age classes and decreased with diameters >50 cm. The reason for this decrease in incidence is uncertain, but it suggests that unlike the decay in sub-alpine fir, it is not associated with the decrease in the number of trees in upper diameter classes. This is more likely due to an increased likelihood of attack by spruce beetle (Furniss and Carolin, 1980) and root rot (Lewis, 1997b).

Both, spruce and fir in this study occurred in clumps. This is expected for several reasons. First, following a stand-initiating event, certain areas within a stand would be more conducive to seed germination and seedling development than others. Secondly, trees that are recruited into treefall gaps would occur in clumps (Kneeshaw and Burton, 1997). Thirdly, at least for spruce, regeneration is more likely to occur on rotten logs and would, therefore, result in a clumped distribution. Spruce in this study did show a higher degree of clumping than was observed in sub-alpine fir.

The distribution pattern of stumps with butt rot reflected the distribution of the host species. Few of the decay fungi discussed above spread by root contact. Therefore, the clumping seen in this study is probably not due to contagion. It is most likely that the apparent clumping is due to the strongly clumped host distribution.

The age-class distributions of spruce and sub-alpine fir indicate that spruce dominate the older age classes and span a range of ages from 60 to 280 years. There is strong evidence for a significant spruce beetle outbreak in the study area ca. 1820 to 1840 (Lindgren and Lewis, 1997). If an outbreak did occur, trees currently 180 years, and older, would have been survivors of the outbreak, whereas younger trees would have been initiated into the stand following this disturbance.

Unlike the Colorado Rockies, where Aplet et al. (1988) observed significant mortality of sub-alpine fir as they approached 300 years of age, sub-alpine fir in the central interior of British Columbia rarely live for >140 to 180 years as demonstrated in Fig. 1. Sub-alpine fir recruitment appears to be continual (Kneeshaw and Burton, 1997 and Fig. 1) as a result of its shade tolerance. As sub-alpine fir gets older and larger, it becomes increasingly susceptible to infection by stem decays which are thought to contribute to mortality of these trees. These minor, single tree disturbances are important for the re-initiation of spruce into the understory as demonstrated by Kneeshaw and Burton (1997).

Spruce is a much longer-lived species in the central interior of B.C., and according to results from this study, is less affected by stem decays. The observed age class distribution, the evidence of a historic beetle outbreak, and the lower decay incidence of spruce collectively indicate that spruce in this area is subject to a different mortality pattern than sub-alpine fir. This mortality pattern reflects infrequent large-scale removal of trees (sometimes selectively in the case of spruce beetle) interspersed with individual tree mortality as a result of endemic spruce beetle and decay fungi.

The data collected in this study indicate a strong relationship between decay incidence in true fir, and a decrease in fir in larger diameter classes. This relationship is not shared by spruce. Additional work on actual gap-makers in these old-growth forests, and sampling of tree species and ages in tree-fall gaps, is required to further describe the contributions of specific fungi to tree-fall, and subsequent ascension to the canopy by understory trees.

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