

# White spruce regeneration following a major spruce beetle outbreak in forests on the Kenai Peninsula, Alaska

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## Abstract

Between 1987 and 2000, a spruce beetle (*Dendroctonus rufipennis*) outbreak infested 1.19 million ha of spruce (*Picea* spp.) forests in Alaska, killing most of the large diameter trees. We evaluated whether these forests would recover to their pre-outbreak density, and determined the site conditions on which spruce germinated and survived following the spruce beetle outbreak in forests of the Anchor River watershed, Kenai Peninsula, Alaska. White spruce (*Picea glauca*) and Lutz's spruce (*Picea × lutzii*), a hybrid between white and Sitka spruce (*Picea sitchensis*), dominate the study area. We measured the pre- and post-outbreak density of spruce in 108 3 m × 80 m plots across the study area by recording all live trees and all dead trees >1.5 m tall in each plot. To determine the fine scale site conditions on which spruce germinated and survived, we measured ground surface and substrate characteristics within 20 cm circular plots around a subset of post-outbreak spruce seedlings. The density of post-outbreak spruce (855/ha) was adequate to restock the stands to their pre-outbreak densities (643/ha) for trees >1.5 m tall. We could not accurately estimate recovery for pre-outbreak spruce seedlings because dead seedlings may have decayed in the 5–18 years since the beetle outbreak occurred. At the fine scale, spruce that germinated post-outbreak grew on a wide variety of substrates including downed log, stump, mesic organic mat, peat, hummocks and mineral soil. They exhibited a strong preference for downed logs (53%) and stumps (4%), and most (91%) of the downed logs and stumps that spruce rooted on were heavily decayed. This preference for heavily decayed logs and stumps was especially evident given that their combined mean cover was only 2% in the 3 m × 80 m plots. Within the 3 m × 80 m plots, spruce seedling survival was negatively correlated with bluejoint (*Calamagrostis canadensis*) litter cover.

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**Keywords:** *Picea glauca*; *Picea × lutzii*; Spruce beetle; *Dendroctonus rufipennis*; *Calamagrostis canadensis*; Decayed logs; Anchor River watershed; Alaska; Spruce regeneration; Forest recovery

## 1. Introduction

Between 1987 and 2000, a spruce beetle (*Dendroctonus rufipennis*) epidemic infested 1.19 million ha of spruce forest in south-central Alaska (USDA Forest Service, and Alaska Department of Natural Resources, 2005). Of the areas impacted, the forests on the southwestern Kenai Peninsula experienced the most substantial reductions in spruce volume,

size class and stand structure (van Hees, 2005). Continuous stands of mature white spruce (*Picea glauca*) and Lutz's spruce (*Picea × lutzii*), which dominated the southwestern Kenai Peninsula prior to the outbreak (Greenberg and Rude, 2003), experienced an 87% reduction in basal area (Boucher and Mead, 2006). While south-central Alaska's forests have experienced periodic outbreaks over the past 250–300 years, this extensive outbreak corresponded to above average summer temperatures that resulted in increased over-winter beetle survival and an acceleration of the beetle maturation rate from 2 years to 1 year (Werner and Holsten, 1985; Berg et al., 2006). The beetle attacks all spruce species that occur in Alaska, but large diameter white spruce and Lutz's spruce are most susceptible to attack (Holsten, 1984; Holsten and Werner, 1990; Werner et al., 2006). The presence of relatively high densities of

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mature large diameter host trees and regional drought-induced stress of these trees may have amplified the outbreak.

Spruce regeneration rates and their sufficiency to restock beetle killed stands in south-central Alaska are in dispute, especially on the Kenai Peninsula. Studies of post-outbreak seedling recruitment in various habitats and locations within south-central Alaska have yielded conflicting results, ranging from little to no recruitment (Holsten et al., 1995; LaBau, 2004; Allen et al., 2006) to recruitment levels capable of restocking the stands (van Hees, 2005; Boucher and Mead, 2006). Site conditions affecting the establishment and regeneration of tree seedlings after the beetle outbreak are important to understanding the dynamics of forest regeneration following this extensive disturbance.

Several factors could potentially influence spruce regeneration following this beetle outbreak. Bluejoint (*Calamagrostis canadensis*) cover typically increases in Kenai Peninsula forest stands disturbed by the spruce beetle (Holsten et al., 1995; LaBau, 2004; Boucher and Mead, 2006) and may competitively inhibit the growth of young spruce on the Kenai Peninsula (Holsten et al., 1995; DeVelice et al., 1999; LaBau, 2004). Boucher and Mead (2006), however, showed no change in spruce regeneration as bluejoint cover increased over time. Exposed mineral soil provides good site conditions for spruce recruitment and is typically associated with root wad tip-ups, mass wasting and fluvial erosion and deposition (Cater and Chapin, 2000; Boggs, 2000). Fires can also provide good site conditions for spruce regeneration (Viereck, 1973; Cater and Chapin, 2000; Fastie et al., 2002), but no major fires have occurred in the Anchor River watershed since 1955. Downed and decomposed logs and stumps can sustain spruce regeneration in other regions (Harmon and Franklin, 1989; DeMeo et al., 1992; Lieffers et al., 1995; DeLong et al., 1997) and previous work on the Kenai Peninsula has shown them to be important sites for post-outbreak regeneration (Davis et al., 2000). It is also possible that extensive spruce mortality could reduce the availability of seed cones, resulting in slow stand regeneration.

Our objectives are to describe the current and pre-outbreak structure of spruce forest stands in the Anchor River basin and to determine if current spruce regeneration is sufficient to restock these stands. Further, we seek to understand the site conditions on which spruce germinate and survive following the outbreak including the relationship between bluejoint cover and spruce regeneration. The results fill significant gaps in our current knowledge of site and vegetation conditions supporting spruce regeneration, and helps resolve some of the conflicting results found by earlier authors concerning forest recovery in bluejoint-dominated sites and the recovery of forests to pre-outbreak densities.

## 2. Methods

### 2.1. Study area

We conducted this study in the Anchor River watershed (583 km<sup>2</sup>) located on the southwestern Kenai Peninsula, Alaska

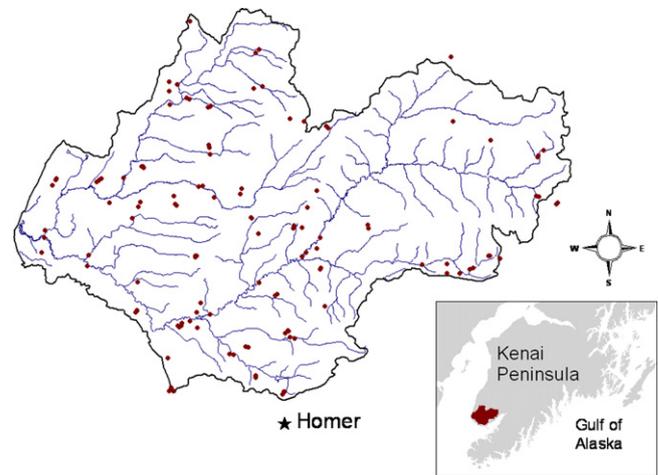


Fig. 1. Map of the study area, the plot locations, and the study area's location on the Kenai Peninsula, Alaska.

(Fig. 1). The climate is transitional between dry continental and wet-mild maritime; average annual precipitation is 750–800 mm near sea level with the wettest months being September through December. The elevation ranges from sea level to 631 m and the higher hills often hold snow into May (Daly, 2002). The topography is hilly upland plateaus with a loess mantle and discontinuous ash layers (Karlstrom, 1964). The drainages are well defined and coalesce into two narrow river floodplains, the Anchor River and Chakok River. Prior to the beetle outbreak, the study area was dominated by continuous stands of white and Lutz's spruce, a common forest type in south-central Alaska (Viereck et al., 1992).

### 2.2. Site selection

We sampled 108 3 m × 80 m ground plots from 66 sites across all forested map classes in the Anchor River watershed. We used stratified systematic sampling to ensure that all forest map classes were sampled (Mueller-Dombois and Ellenberg, 1974; Steel and Torrie, 1960). The strata, based on forest map classes from a 1:30,000 aerial photo-interpreted landcover map (Greenberg and Rude, 2003), were woodland spruce (10–24% canopy cover), open spruce (25–59%), closed spruce (60–100%) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*, 10–100%). The cover estimates included live trees and standing dead. We systematically selected the 66 sites by overlaying a digital grid on the Greenberg and Rude (2003) map; we extrapolated the GPS location for each grid intersection and sampled one or more plots at each of these 66 sites.

### 2.3. Field sampling

Because locating young spruce within thick ground cover (mostly bluejoint) was difficult, we conducted field sampling after senescence and before snowfall in the fall of 2004 and after snowmelt and before green-up in the spring of 2005. We accessed the sites by road, ATV and hiking. For taxonomic purposes, we treated white and Lutz's spruce as the same

species (white spruce) because identifying seedlings and snags to species was not always possible. The taxonomy follows the Integrated Taxonomic Information System (2008).

### 2.3.1. Coarse scale 3 m × 80 m plots

We used 3 m × 80 m plots to measure current and pre-outbreak forest structure in relation to site characteristics. At each of the 66 field sites, we set up one 3 m × 80 m plot oriented perpendicular to the slope or, when on a floodplain, perpendicular to the stream channel (Elzinga et al., 1998). We moved a plot if it showed any evidence of human disturbance or if the vegetation was not homogeneous in both composition and structure. We also sampled additional map classes (Greenberg and Rude, 2003) found closest to the original plot (total of 108 plots). After we encountered an additional map class, the beginning of the new plot was determined by walking 50 m along a random compass bearing.

For each plot, we recorded aspect, slope, elevation and dominant understory species. We recorded the following data for each live tree >1.5 m in height: distance along the plot, height, diameter at breast height (dbh) and the presence/absence of seed bearing cones. For two randomly selected trees in each 3 m × 80 m plot, we measured tree height with a clinometer and measuring tape; we estimated the heights of all remaining trees. For each standing dead tree >1.5 m tall we collected the above information plus indexed the tree's decay class using Harmon et al.'s (2005) decomposition stages ranging from 1 = un-decayed to 5 = heavily decayed. We also inferred whether trees were beetle killed by the presence of larval galleries in the cambium. Within each plot, we collected cores (increment borer) from the base of five live and five dead trees representing a range of sizes; we later used these cores to age the trees. For each live spruce ≤1.5 m tall (referred to as spruce seedlings), we recorded its height and distance along the 3 m × 80 m plot. On a random subset of 64 of the 108 3 m × 30 m plots, we recorded whether each spruce ≤1.5 m tall was rooted on organic soil, mineral soil, downed log or stump.

Another desired density measure was that of pre-outbreak seedlings. This count requires recording both live and dead seedlings per plot. We did not, however, record dead seedlings because they may have decomposed post-outbreak and thus we would not be able to obtain an accurate dead seedling count.

We determined ground cover within each 3 m × 80 m plot by sampling five systematically placed (16 m spacing) 1 m × 1 m subplots (Fig. 2). We visually estimated the percent cover (Brown, 1954; Daubenmire, 1959) of the following variables: bluejoint leaves that had died within a year of sampling (referred to as bluejoint litter), fine litter not including bluejoint litter (conifer needles and finer), coarse litter not including bluejoint litter (leaves, twigs <2.4 cm diameter), small wood (2.4–7.2 cm diameter), downed logs (>7.2 cm diameter) by decay class, moss, lichen, mineral soil, rock and water.

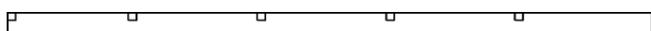


Fig. 2. Diagram of a 3 m × 80 m plot including the five 1 m × 1 m subplots.

### 2.3.2. Fine scale 20 cm plots

To measure more precise site characteristics on which individual spruce germinated and survived following the outbreak, we collected data on the first spruce seedling (i.e. ≤1.5 m tall) encountered within each 3 m × 80 m plot (referred to as random post-outbreak seedling). We assumed in the field that spruce ≤1.5 m tall had germinated post-outbreak, however, only 57 of the 108 seedlings had germinated post-outbreak. We recorded its height and determined its age by cutting the spruce at its base and counting the rings. Within a 20 cm diameter of this spruce, we visually estimated the ground cover of the following variables: bluejoint litter, fine litter, coarse litter, small wood, downed log, stump, moss, lichen, mineral soil, water, peat and hummock. Peat was defined as a wet organic horizon and surface typically dominated by sedges, *Sphagnum* species and other mosses. Hummocks were organic mounds raised above the ground 20 cm or more and typically supported ericaceous shrubs, bluejoint, sedges, *Sphagnum* species and other mosses. We also recorded the decay class of each log and stump. We used a spade to dig a 10 cm soil pit within 1 cm of each random post-outbreak seedling representing the initial rooting depth of seedlings. Substrate information included organic matter depth, mineral soil depth, soil texture, water table depth and pH.

To ensure that we sampled an adequate number of post-outbreak seedlings from each of the above ground cover types, we subjectively selected four additional post-outbreak spruce in each 3 m × 80 m plot, focusing on rare types such as exposed mineral soil and stumps. For each of these seedlings we recorded the same information as recorded for the random post-outbreak seedling.

## 2.4. Data analysis

### 2.4.1. Vegetation and site description from 3 m × 80 m plots

We determined the mean and range for the site (aspect, slope and elevation) and vegetation (tree height, dbh, cover of live spruce and standing beetle killed spruce, and dominant understory species) information from each 3 m × 80 m plot. We also averaged (±S.E.) the mean cover for each variable in each 1 m × 1 m subplot to determine mean cover per 3 m × 80 m plot.

### 2.4.2. Pre- and post-outbreak stand structure

To characterize current (i.e., post-outbreak) spruce stand structure, we summed the total number of live trees >1.5 m tall and seedlings from each 3 m × 80 m plot into the following dbh classes: 0–10 cm, 10–20 cm, 20–30 cm and >30 cm. To characterize the pre-outbreak spruce stand structure, we summed all live and beetle killed trees according to the same dbh classes. We expressed all densities as trees per ha. We did not record dead seedlings in the field and, consequently, they were not included in the beetle killed spruce 0–10 cm class.

We calculated seedling regeneration on a per ha basis. At many sites seedlings had a clumped distribution where more spruce germinated in a small area than could be expected to

survive to maturity. Therefore, to determine if current spruce seedling densities were sufficient to restock forest stands to pre-outbreak densities, we needed realistic estimates of the number of spruce seedlings that could actually survive. We assumed that the number of spruce seedlings that could survive to maturity in any 1 m × 3 m plot section equaled the average number of >10 cm dbh trees supported pre-outbreak.

#### 2.4.3. Coarse scale site conditions supporting spruce regeneration

In the 3 m × 80 m plots, to understand the relationship between the percent cover of bluejoint litter and the density of post-outbreak spruce seedlings required that we first determine the year the overstory died in each 3 m × 80 m plot and then identify the number of spruce that germinated following stand death. For 93 of the plots we could determine the year the spruce overstory died by overlaying (using ArcGis) our plots over an insect outbreak shapefile which gave the year and degree of stand infestation (USDA Forest Service, and Alaska Department of Natural Resources, 2005). These estimated infestation degrees varied from light to moderate to high and we considered years with infestation rates of moderate to high to have killed the stands. For 15 plots, we could not determine the year of infestation because either the plot fell on the edge of an insect infestation polygon or the trees in the plot died slowly over numerous years. For these plots, we assigned 1999 as the year of stand death because 96% of the stands were moderately to heavily infested in the Anchor River watershed by this date.

To identify the number of spruce that germinated following the death of the stand, we needed to know the age of all seedlings in the plots. Having not aged all seedlings directly, we estimated the age of each seedling using a regression of age versus height ( $p < 0.001$ ;  $r^2 = 56.7\%$ ;  $y = 0.1814 + 0.0350x$ ; 50% PI) based on the five spruce seedlings that we sampled in each 3 m × 80 m plot. Based on the regression, we excluded trees that were older than the year each stand died. Stands died at various ages (1990–2001) so the height/age cutoff point from the regression varied per plot. We used a 50% predictive interval (PI) around the regression line as the upper limit for excluding seedlings that had germinated prior to the stand's death.

To refine our understanding of the relationship between bluejoint litter cover and seedling abundance, we hypothesized that bluejoint litter inhibited spruce regeneration above a coverage threshold of approximately 60%. We used 60% because of an observed break in the data (Fig. 4). As such, we tested the null hypothesis that seedling abundance in stands with >60% coverage of bluejoint litter was equal to seedling abundance in stands with <60% coverage of bluejoint litter. Due to excessive zeros and a wildly fluctuating residual error variance, our seedling abundance data do not conform to any standard statistical model. Therefore, we assessed the relationship between seedling abundance and bluejoint litter cover with a nonparametric procedure (i.e. bootstrapping; Hjorth, 1994). Graphically, tree density values appear lower on average above a “threshold” grass cover of 60%. Thus we defined the

following test statistic ( $T_{\text{true}}$ ):

$$T_{\text{true}} = \overline{d_{g < 60\%}} - \overline{d_{g > 60\%}} \quad (1)$$

where  $d$  is spruce seedling density and  $g$  is bluejoint litter cover. Then, randomly and with replacement, we sampled  $n$  cases from the density data. Replacing the actual data with the re-sampled values allowed us to calculate  $T_{\text{sim}}$  as in (1). We generated 10,000 simulated datasets, calculated  $T_{\text{sim}}$  for each dataset and tallied the number of datasets giving  $T_{\text{sim}} > T_{\text{true}}$ . We calculated the  $p$ -value ( $p$ ) of interest as:

$$p = \frac{E}{10,000} \quad (2)$$

where  $E$  is the number of simulated datasets for which  $T_{\text{sim}} > T_{\text{true}}$ . This  $p$ -value corresponds to a one-tailed hypothesis test of  $\overline{d_{g < 60\%}} = \overline{d_{g > 60\%}}$ .

#### 2.4.4. Fine scale site conditions supporting spruce regeneration

To understand fine scale site conditions that favored seedling regeneration, we evaluated the substrates and ground cover that supported the five post-outbreak spruce (four subjectively sampled post-outbreak spruce plus the random post-outbreak seedling) per 3 m × 80 m plot. We identified the dominant substrate in each soil pit and grouped them according to the following types: downed log, stump, mesic organic mat, peat, hummock and mineral soil. Then we determined the mean ( $\pm$ S.E.) organic matter depth, ground surface types, wood decay class and pH by substrate type.

### 3. Results

#### 3.1. Vegetation and site description from 3 m × 80 m plots

Most (103 of the 108 plots) stands were dominated by white spruce; other tree species such as paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) were uncommon (<1% cover). The total cover of spruce (live plus standing beetle killed) ranged from 10% to 80% and, of that total, standing beetle killed spruce cover ranged from 1% to 60% and live tree cover from 2% to 70%. The largest white spruce dbh was 71 cm and the tallest spruce was 36 m. The oldest live spruce was 140 years old and the oldest beetle killed spruce was 220 years old. The plots occurred on slopes from 0° to 40° on all aspects, the elevation ranged from 11 to 500 m and all sites were mesic but some had small inclusions of wet peat.

Black cottonwood and white spruce were co-dominant in five plots. In these plots, the largest black cottonwood dbh was 71 cm and the tallest was 29 m; the largest white spruce dbh was 33 cm and the tallest was 18 m. The plots occurred on both floodplains and sideslopes and the slope ranged from 1° to 28° on all aspects.

Because we sampled before and after green-up we could not accurately record understory plant species composition, but we did record senescent vegetation. The dominant species were mountain alder (*Alnus incana* ssp. *tenuifolia*), Barclay's willow

Table 1

Mean percent ( $\pm$ S.E.) ground cover from the 1 m  $\times$  1 m subplots averaged per 3 m  $\times$  80 m plot ( $n = 108$  plots)

Ground surface	Ground cover (%)
Bluejoint litter	35.0 $\pm$ 1.9
Moss	20.4 $\pm$ 1.4
Lichen	0.5 $\pm$ 0.0
Fine litter (pine needles and finer)	6.4 $\pm$ 0.8
Coarse litter (leaves, twigs <2.4 cm diameter)	28.7 $\pm$ 1.2
Small wood (2.4–7.2 cm)	2.3 $\pm$ 0.3
Downed logs: decay class 1	2.8 $\pm$ 0.3
Downed logs: decay class 2	3.9 $\pm$ 0.3
Downed logs: decay class 3	1.7 $\pm$ 0.3
Downed logs: decay class 4	0.9 $\pm$ 0.1
Downed logs: decay class 5	1.1 $\pm$ 0.1
Basal area	1.8 $\pm$ 0.2
Exposed mineral soil	0.3 $\pm$ 0.1
Rock	0.2 $\pm$ 0.0
Water	0.7 $\pm$ 0.1

(*Salix barclayi*), bluejoint, fireweed (*Chamerion angustifolium*), spreading woodfern (*Dryopteris expansa*), western oakfern (*Gymnocarpium dryopteris*), splendid feather moss (*Hylocomium splendens*) and Schreber's big red stem moss (*Pleurozium schreberi*).

The dominant ground covers in the 1 m  $\times$  1 m plots (all 3 m  $\times$  80 m plots combined) were bluejoint litter (35.0  $\pm$  1.9% S.E.), coarse litter (28.7  $\pm$  1.2% S.E.) and moss (20.4  $\pm$  1.4% S.E.) (Table 1). The total cover of downed logs >7.2 cm diameter (combined decay classes 1–5) was 10.4%, and of these downed logs, most (6.7%) were relatively un-decayed (combined decay classes 1 and 2). Other ground cover types such as exposed mineral soil and rock were rare (0.3  $\pm$  0.1% S.E. and 0.2  $\pm$  0.0% S.E., respectively). The only newly exposed mineral soil in the plots was from fluvial deposition and erosion.

### 3.2. Pre- and post-outbreak stand structure

Live spruce density was highest in the 0–10 cm dbh class and declined in density in each subsequent dbh class (Fig. 3). The total density of live spruce in the 0–10 cm class was 1561/ha. After adjusting for overcrowding (maximum of 1.32 spruce/1 m  $\times$  3 m section), the projected density was 615/ha. When this thinned seedling density was combined with the density of larger size classes (240/ha), the total projected post-outbreak live spruce density was 855/ha.

The density of beetle killed spruce (standing plus downed) was lowest in the 0–10 cm dbh class and was likely due to our inability to record dead spruce seedlings in the field. The density of beetle killed spruce >1.5 m tall was 403/ha. Our estimate of pre-outbreak live spruce >1.5 m tall is 643/ha and was determined by summing the density of beetle killed spruce >1.5 m tall (403/ha) and the density of live spruce >1.5 m tall (240/ha).

### 3.3. Coarse scale site conditions supporting spruce regeneration

The mean number of spruce seedlings in all 3 m  $\times$  80 m plots was 24.9  $\pm$  10.4 S.E. with a range of 0–420 ( $n = 108$ ).

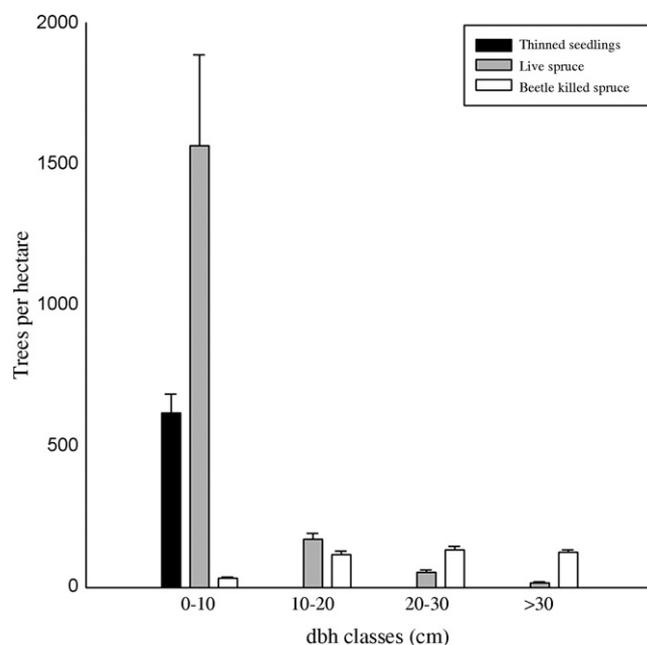


Fig. 3. Spruce density by dbh class of live spruce and beetle killed spruce ( $n = 108$  plots). The thinned seedling column is the spruce density after adjusting for overcrowding (maximum of 1.32 spruce/1 m  $\times$  3 m section). Note that the beetle killed spruce 0–10 dbh class does not include beetle killed spruce  $\leq 1.5$  m tall.

Fig. 4 shows the relationship of the number of post-outbreak spruce seedlings to increasing bluejoint litter cover. Our bootstrapping test indicated that seedling abundance was significantly greater in plots with bluejoint litter coverage less than a threshold value of 60% ( $p = 0.04$ ). The mean number of spruce seedlings in plots with <60% bluejoint litter coverage was 27.2 ( $n = 98$ ) while plots with >60% bluejoint litter coverage averaged 2.4 seedlings ( $n = 10$ ).

### 3.4. Fine scale site conditions supporting spruce regeneration

As stated earlier, of the 108 random post-outbreak seedlings sampled, only 57 were young enough to have germinated following the death of their respective forest stands and only

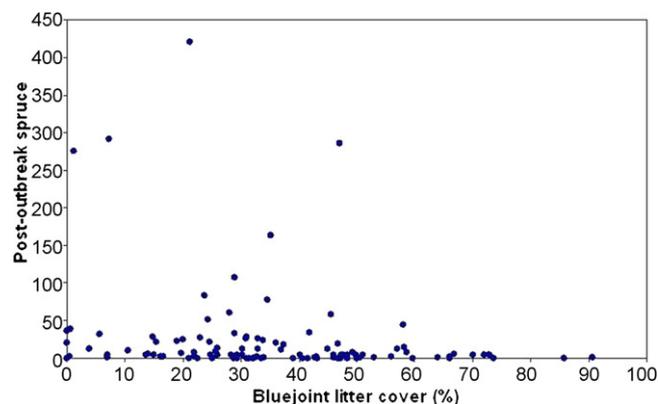


Fig. 4. The relationship of the number of post-outbreak spruce to bluejoint litter cover in the 3  $\times$  80 m plots.

Table 2  
The percent of different soil substrates that support spruce regeneration and the adjacent ground cover

Substrate or ground cover type	Substrates supporting spruce regeneration		Ground cover (mean $\pm$ S.E.)
	3 m $\times$ 80 m plots (mean % $\pm$ S.E.)	20 cm plots (%)	
<i>n</i>	42 plots, 752 spruce	57 spruce	57 spruce
Substrate			
Downed log	44 $\pm$ 7	53	
Stump	12 $\pm$ 4	4	
Organic mat <sup>a</sup>	44 $\pm$ 7	42	
Mesic organic mat	–	28	
Peat	–	7	
Hummock	–	7	
Mineral soil	0	2	
Ground cover			
Bluejoint litter			11.7 $\pm$ 2.1
Moss			49.9 $\pm$ 3.5
Lichen			2.5 $\pm$ 1.4
Fine litter (conifer needles and finer)			7.1 $\pm$ 1.8
Coarse litter (leaves, twigs <2.4 cm)			26.4 $\pm$ 2.9
Small wood (2.4–7.2 cm)			1.4 $\pm$ 2.0
Exposed mineral soil			0.1 $\pm$ 0.1
Rock			0
Water			0

The substrate data are from two sources: 64 3 m  $\times$  80 m plots (only 42 plots had seedlings) and 57 randomly sampled post-outbreak seedlings (20 cm diameter plots).

<sup>a</sup> This measure combines the mesic organic mat, peat and hummock categories.

these seedlings were included in the analysis. The 20 cm diameter plots surrounding these seedlings show them to be growing on a wide variety of substrates including downed log, stump, mesic organic mat, peat, hummocks and mineral soil (Table 2). Most (53%) were rooted on downed logs and these logs tended to be heavily decayed; 91% were in decay classes 4 and 5 while the remaining 9% were in decay class 3. Mesic organic mats were the second most common substrate for regeneration, supporting 28% of post-outbreak seedlings. These organic mats were >10 cm deep over mineral soil. The dominant ground covers in the 20 cm diameter plots were moss (49.9  $\pm$  3.5% S.E.), coarse litter (26.4  $\pm$  2.9% S.E.) and bluejoint litter (11.7  $\pm$  2.1% S.E.).

For the 64 3 m  $\times$  80 m plots, we recorded whether post-outbreak seedlings were rooted on organic soils, mineral soils, downed logs or stumps. A total of 752 seedlings were recorded in 42 of the plots, with the remainder of the plots having no seedlings. The average percent occurrence of seedlings on each substrate was determined per plot and averaged ( $\pm$ S.E.) across all 42 plots (Table 2). Seedlings were equally distributed between heavily decayed downed logs (44  $\pm$  7%) and organic

mats (44  $\pm$  7%), 12  $\pm$  4% on heavily decayed stumps and none on exposed mineral soil. These values were similar to those derived from the 20 cm plot data (downed log = 53%, organic mat (including mesic organic, peat and hummock) = 42%, stump = 4% and mineral soil = 2%; Table 2).

Table 3 gives the average of substrate characteristics for the five post-outbreak seedlings sampled per 3 m  $\times$  80 m plot. Of the 540 seedlings sampled, 263 germinated post-outbreak. Downed logs and stumps that supported post-outbreak spruce had a high level of consistency in terms of mean pH at 5 cm depth (both 4.5), range in pH (3.1–6.3 and 3.6–6.3, respectively), depth of organic matter (4.4 and 2.7, respectively) and the percentage of spruce rooted directly on decayed wood (14% and 19%, respectively; not given in table). Post-outbreak spruce also exhibited a strong preference for logs and stumps in decay classes 3–5 (Table 4).

The pH at 5 cm depth on mesic organic mats >10 cm thick that supported post-outbreak spruce was 4.8  $\pm$  0.1 S.E. (Table 3). Peat occurred in small wet depressions within the larger matrix of mesic organic mats. For post-outbreak spruce occurring on peat, the pH was 4.8  $\pm$  0.2 S.E. Hummocks

Table 3  
The mean ( $\pm$ S.E.) organic matter (litter, duff and organic mat) depth and pH by soil substrate supporting spruce regeneration (data from the five post-outbreak spruce sampled per 3 m  $\times$  80 m plot)

Soil characteristics	Substrate supporting spruce regeneration					
	Downed log	Stump	Mesic organic mat	Peat	Hummock	Mineral soil
<i>n</i>	95	21	102	12	25	8
Organic matter depth (cm) (mean $\pm$ S.E.)	4.4 $\pm$ 0.4	2.7 $\pm$ 0.7	10 $\pm$ 0	10 $\pm$ 0	10 $\pm$ 0	0
pH at 5 cm (mean $\pm$ S.E.)	4.5 $\pm$ 0.1	4.5 $\pm$ 0.2	4.8 $\pm$ 0.1	4.8 $\pm$ 0.2	4.9 $\pm$ 0.1	5.2 $\pm$ 0.2
pH range	3.1–6.3	3.6–6.3	3.5–6.6	4.0–6.0	3.9–6.0	4.5–5.8

The soil pits were 10 cm deep.

Table 4

The percent of spruce occurring on the five log decay classes ranging from 1: un-decayed to 5: heavily decayed (Harmon et al., 2005) (data from the five post-outbreak spruce sampled per 3 m × 80 m plot)

Substrate	Decay class					n
	1	2	3	4	5	
Nurse log	0	2	16	37	46	57
Stump	0	0	40	10	50	10

occurred as small inclusions on mesic organic mats and on peat deposits. On hummocks supporting post-outbreak spruce, the pH was  $4.9 \pm 0.1$  S.E. For the few ( $n = 8$ ) post-outbreak spruce sampled on mineral soil, the top 10 cm was either an A horizon ( $n = 2$ ) or C horizon ( $n = 6$ ), with a pH of  $5.2 \pm 0.2$  S.E.

### 3.5. Cone bearing trees

Of the 882 live spruce trees >1.5 m tall recorded in the plots, 22% were cone bearing (Table 5). The percentage of cone bearing trees increased with increasing dbh from the ≤5 cm dbh class (4%) through the 16–20 cm dbh size class (44%). The highest percentage occurred in the 41–45 cm class (67%).

## 4. Discussion

### 4.1. Vegetation and site conditions supporting spruce regeneration

Various site and vegetation characteristics influence post-outbreak spruce regeneration. One is the loss of seed source due to the death of the mature spruce trees. Most of the current live trees are less than 10 cm dbh and the percentage of cone bearing trees is low in this size class. However, the percentage of cone bearing trees increases through the 16–20 cm dbh size class and, consequently, we expect the percentage of cone bearing trees to increase as the forests mature.

Exposed mineral soil provides good site conditions for spruce recruitment (Cater and Chapin, 2000; Boggs, 2000). However, it was uncommon (0.3%) in the study plots and only associated with river erosion and deposition (Table 1). Given the ubiquity of snags on the Kenai, we expected tree fall to be

common resulting in extensive tip-ups and exposed mineral soil. However, we did not record root tip-ups in the plots although we observed them occasionally outside the plots. Micales et al. (2004) found that most tree falls on the Kenai Peninsula are caused by breakage of the tree trunk rather than uprooting of the whole tree. The trunks snap off several feet above the ground due to a weakening of the tree bole by wood rot fungi.

In boreal Alaska, fires provide good site conditions for the establishment of black spruce (*Picea mariana*), white spruce and paper birch seedlings (Viereck, 1973; Cater and Chapin, 2000; Fastie et al., 2002). We did not, however, observe evidence of fire in our study plots. We expected this given the reported mean fire return interval of 400–600 years in upland forests of white and Lutz's spruce on the Kenai Peninsula (Berg and Anderson, 2006; Berg et al., 2006). This mean fire return interval, however, may shorten due to an increase in human presence on the Kenai Peninsula.

A factor that may reduce post-outbreak spruce regeneration is an increase in bluejoint cover. LaBau (2004), Holsten et al. (1995) and Boucher and Mead (2006) all indicated that bluejoint cover increases post-outbreak and either has a negative or neutral correlation with spruce regeneration. We did not directly measure change in bluejoint cover over time as did LaBau (2004), Holsten et al. (1995) and Boucher and Mead (2006), but our bootstrapping test supports the negative relationship between spruce regeneration and bluejoint litter cover in the 3 m × 80 m plots. In the 20 cm plots, mean bluejoint cover was one-third that of its mean cover in the 3 m × 80 m plots again suggesting a negative relationship. We speculate that this relationship may be less pronounced in the 3 m × 80 m plots because the plots are large and heterogeneous supporting a variety of soil substrates and ground surfaces that influence spruce regeneration.

We found that downed and heavily decayed logs and stumps are excellent substrates for spruce regeneration. This preference for heavily decayed logs and stumps is especially evident given that their combined mean cover is only 2% in the 3 m × 80 m plots, yet 57% (20 cm plots) and 44% (3 m × 80 m plots) of post-outbreak spruce rooted on these substrates. Other studies have shown this preference for downed and decomposed logs on the Kenai Peninsula (Davis et al., 2000), in the maritime rainforests of the Pacific Northwest (Harmon and Franklin, 1989; DeMeo et al., 1992) and white spruce forests of Western Canada (Lieffers et al., 1995; DeLong et al., 1997). Davis et al. (2000) reported 95% of spruce <20 cm in height rooted on decayed logs two years post-outbreak on a portion of the Kenai Peninsula, and Lieffers et al. (1995) reported roughly 32% of understory spruce in Alberta were on rotten logs.

Suitable sites for spruce regeneration may not occur in some stands partly due to high bluejoint cover and a lack of heavily decayed downed logs. All sampled stands do, however, have un-decayed downed logs, stumps or standing dead trees. To date, only 10% of standing dead trees have fallen and the average ground cover for un-decayed downed logs or stumps is high at 6.7%. Consequently, understanding the decay rate for beetle killed trees is important for understanding the rates by

Table 5

Percent of trees ( $n = 882$ ) that were cone bearing by dbh size class

Spruce dbh (cm)	% cone bearing	n
≤5	4	208
6–10	10	232
11–15	23	156
16–20	44	135
21–25	44	77
26–30	54	41
31–35	47	19
36–40	33	6
41–45	67	3
46–65	60	5

which spruce forests recover from spruce beetle mortality. Harmon et al. (2005) examined the decay rates of dead Lutz's spruce on the Kenai. Recently fallen logs take approximately 70 years to fully decay (mean wood densities of 0.39–0.11 g cm<sup>3</sup>, respectively), and for snags the mean wood densities ranged from 0.42–0.39 g cm<sup>3</sup> indicating minor decay if they remain standing. In time, the snags will fall and the downed logs and stumps will decay providing suitable sites for spruce regeneration even in stands with high bluejoint litter cover.

#### 4.2. Forest management considerations

A major forest management concern in Alaska is whether current tree and seedling densities are sufficient to restock forest stands to pre-outbreak densities with various studies giving contradictory results (Boucher and Mead, 2006; Holsten et al., 1995; LaBau, 2004; van Hees, 2005). Our results indicate that post-outbreak live spruce densities are adequate to restock the stands to their pre-outbreak densities for spruce >1.5 m tall. We could not accurately estimate recovery for spruce seedlings because dead seedlings might have decayed in the 5–18 years since the beetle outbreak occurred. Assuming that all post-outbreak live spruce survive over time, then their density (855/ha) is more than adequate to restock spruce >1.5 m tall to their pre-outbreak density of 643/ha.

In actively managed forests (salvage logging, scarification), managers should be aware that spruce regeneration is higher on downed heavily decayed wood. Even in stands with high bluejoint litter cover the forests will likely recover due to the presence of substrates such as downed wood that upon decaying support young spruce.

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#### References

Allen, J.L., Wesser, S., Markon, C.J., Winterberger, K.C., 2006. Stand and landscape level effects of a major outbreak of spruce beetles on forest vegetation in the Copper River Basin, Alaska. *Forest Ecology and Management* 227, 257–266.

Berg, E.E., Anderson, R.S., 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska, over the last two millennia as determined from soil charcoal. *Forest Ecology and Management* 227, 275–283.

Berg, E.E., Henry, J.D., Fastie, C., De Volder, A.D., Matsuoka, S.M., 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane

National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227, 219–232.

Boggs, K.W., 2000. Classification of community types, successional sequences, and landscapes of the Copper River Delta, Alaska. USDA Forest Service Pacific Northwest Research Station, Portland (OR). General Technical Report PNW-GTR-469.

Boucher, T.V., Mead, B.R., 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987–2000. *Forest Ecology and Management* 227, 233–246.

Brown, D., 1954. Methods of surveying and measuring vegetation. Commonwealth Agricultural Bureau, Bulletin 42, Bucks, England.

Cater, T.C., Chapin III, F.S., 2000. Differential effects of competition or microenvironment on boreal tree seedling establishment after fire. *Ecology* 81, 1086–1099.

Daly, C., 2002. Alaska average monthly or annual precipitation, 1961–90. Spatial Climate Analysis Service, Oregon State University, Corvallis.

Daubenmire, R.D., 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33, 43–66.

Davis, J.D., Wiedmer, M., Hill, D., 2000. Vegetation survey and moose use of the South Ninilchik Block, Kenai Peninsula. Technical Report No. 00-06, Alaska Department of Fish and Game, Anchorage, AK.

DeLong, H.B., Lieffers, V.J., Blenis, P.V., 1997. Microsite effects on first year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27, 1452–1457.

DeMeo, T., Martin, J., West, R.A., 1992. Forest plant association management guide: Ketchikan Area, Tongass National Forest. USDA Forest Service Alaska Region, Juneau (AK). General Technical Report R10-MB-210.

DeVelice, R., Hubbard, C., Boggs, K., Boudreau, S., Potkin, M., Boucher, T., Wertheim, C., 1999. Plant community types of the Chugach National Forest: southcentral Alaska. USDA Forest Service Chugach National Forest, Alaska Region, Anchorage (AK). Tech. Pub. R10-TP-76.

Elzinga, C.L., Salzer, D.W., Willoughby, J.W., 1998. Measuring and monitoring plant populations. USDI Bureau of Land Management, Denver (CO). BLM/RS/ST-98/005 + 1730.

Fastie, C.L., Lloyd, A.H., Doak, P., 2002. Fire history and post-fire forest development in an upland watershed of interior Alaska. *Journal of Geophysical Research* 108, 8150.

Greenberg, G., Rude, M., 2003. Kenai Peninsula vegetation: Kenai 18. Kenai Peninsula ecosystem level vegetation mapping initiative. Available online at [http://www.borough.kenai.ak.us/sbb/pages/gis\\_pages/vegclass.html](http://www.borough.kenai.ak.us/sbb/pages/gis_pages/vegclass.html) (accessed 6 August 2007).

Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. *Ecology* 70 (1), 48–59.

Harmon, M., Fasth, B., Yatskov, M., Sexton, J., Trummer, L., 2005. The fate of dead spruce on the Kenai Peninsula: a preliminary report. USDA Forest Service Technical Report R10-TP-134.

Holsten, E.H., 1984. Factors of susceptibility in spruce beetle attack on white spruce in Alaska. *Journal of the Entomological Society of British Columbia* 81, 39–45.

Holsten, E.H., Werner, R.A., 1990. Comparison of white, Sitka, and Lutz spruce as hosts of the spruce beetle in Alaska. *Canadian Journal of Forest Research* 20, 292–297.

Holsten, E.H., Werner, R.A., DeVelice, R., 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environmental Entomology* 24, 1539–1547.

Hjorth, J.S.U., 1994. Computer Intensive Statistical Methods. Chapman & Hall, London, England.

Integrated Taxonomic Information System, 2008. <http://www.itis.gov/>.

Karlstrom, T.N.V., 1964. Quaternary geology of the Kenai Lowland and glacial history of the Cook Inlet region, Alaska. U.S. Geological Survey Professional Paper 443, Washington, DC.

LaBau, J., 2004. Synthesis of ENRI findings from 5 years of study of the spruce bark beetle on the Kenai Peninsula [abstract]. In: A changing Alaskan ecosystem [symposium cd-rom], 2004 Feb 24–26; Homer, Alaska. Kenai Peninsula Borough, Kenai Peninsula (AK), Spruce Beetle Mitigation Program.

- Lieffers, V.J., Stadt, K.J., Navratil, S., 1995. Age structure and growth of understory white spruce under aspen. *Canadian Journal of Forest Research* 26, 1002–1007.
- Micales, J., Banik, M., Trummer, L., 2004. Wood decay fungi of spruce in south-central Alaska [poster]. In: A changing Alaskan ecosystem [symposium cd-rom], 2004 Feb 24–26; Homer, Alaska. Kenai Peninsula Borough, Kenai Peninsula (AK), Spruce Beetle Mitigation Program.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, Inc., New York.
- Steel, R.G.D., Torrie, J.H., 1960. *Principles and Procedures of Statistics*. McGraw-Hill Book Company, Inc., New York (NY).
- USDA Forest Service, State and Private Forestry, Forest Health Protection, Alaska Department of Natural Resources, Division of Forestry. 2005. Shapefile\_akdamage04. Forest insect and disease conditions in Alaska (shapefile\_akdamage04). Available from: <http://agdc.usgs.gov/data/projects/fhm/#K>.
- van Hees, W.S., 2005. Spruce reproduction dynamics on Alaska's Kenai Peninsula, 1987–2000. USDA Forest Pacific Northwest Research Station, Portland (OR). Res. Pap. PNW-RP-563, 18 p.
- Viereck, L.A., 1973. Wildfire in the taiga of Alaska. *Journal of Quaternary Research* 3, 465–495.
- Viereck, L., Dryness, C., Batten A., Wenzlick, K., 1992. The Alaska vegetation classification. General Technical Report PNW-GTR-286. Portland, Oregon. U.S. Forest Service, Pacific Northwest Research Station, 278 p.
- Werner, R.A., Holsten, E.H., 1985. Effect of phloem temperature on development of spruce beetles in Alaska. In: Safrankik, L. (Ed.), *The Role of the Host in the Population Dynamics of Forest Insects*. Canadian Forest Service, Pacific Forestry Centre, Victoria (British Columbia, Canada), pp. 155–163.
- Werner, R.A., Holsten, E.H., Matsuoka, S.M., Burnside, R.E., 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *Forest Ecology and Management* 227, 195–206.