

Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987–2000

Tina V. Boucher*, Bert R. Mead

U.S. Forest Service, Pacific Northwest Research Station, Forest Inventory and Analysis, 3301 C Street, Suite 200, Anchorage, AK 99503, USA

Abstract

Forests of the Kenai Peninsula, Alaska experienced widespread spruce (*Picea* spp.) mortality during a massive spruce beetle (*Dendroctonus rufipennis*) infestation over a 15-year period. In 1987, and again in 2000, the U.S. Forest Service, Pacific Northwest Research Station, Forest Inventory and Analysis Program conducted initial and remeasurement inventories of forest vegetation to assess the broad-scale impacts of this infestation. Analysis of vegetation composition was conducted with indirect gradient analysis using nonmetric multidimensional scaling to determine the overall pattern of vegetation change resulting from the infestation and to evaluate the effect of vegetation change on forest regeneration. For the latter we specifically assessed the impact of the grass bluejoint (*Calamagrostis canadensis*) on white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) regeneration. Changes in vegetation composition varied both in magnitude and direction among geographic regions of the Kenai Peninsula. Forests of the southern Kenai Lowland showed the most marked change in composition indicated by relatively large distances between 1987 and 2000 measurements in ordination space. Specific changes included high white spruce mortality (87% reduction in basal area of white spruce >12.7 cm diameter-at-breast height (dbh)) and increased cover of early successional species such as bluejoint and fireweed (*Chamerion angustifolium*). Forests of the Kenai Mountains showed a different directional change in composition characterized by moderate white spruce mortality (46% reduction) and increased cover of late-successional mountain hemlock (*Tsuga mertensiana*). Forests of the Gulf Coast and northern Kenai Lowland had lower levels of spruce mortality (22% reduction of Sitka spruce (*Picea sitchensis*) and 28% reduction of white spruce, respectively) and did not show consistent directional changes in vegetation composition. Bluejoint increased by $\geq 10\%$ in cover on 12 of 33 vegetation plots on the southern Kenai Lowland but did not increase by these amounts on the 82 plots sampled elsewhere on the Kenai Peninsula. Across the Kenai Lowland, however, regeneration of white spruce and paper birch did not change in response to the outbreak or related increases in bluejoint cover from 1987 to 2000. Although some infested areas will be slow to reforest owing to few trees and no seedlings, we found no evidence of widespread reductions in regeneration following the massive spruce beetle infestation.

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1. Introduction

The spruce beetle is the most significant insect agent of spruce mortality in boreal forests (Werner and Holsten, 1982; Werner et al., 2006). Between 1987 and 2003 over 824,000 ha of forests were infested by spruce beetles in south-central Alaska; 429,000 ha of which were on the Kenai Peninsula (U.S. Forest Service, 2004; M. Rude, Kenai Peninsula Spruce Bark Beetle Mitigation Program, unpublished data). In a typical infestation, spruce beetles preferentially breed in and kill the large-diameter, slowly growing spruce (Hard et al., 1983;

Holsten, 1984; Hard, 1985, 1987). The recent outbreak initially followed this pattern but intensified to epidemic levels in the 1990s when it caused mortality of smaller-diameter spruce and stand replacing disturbances on parts of the Kenai Peninsula. Although spruce beetle outbreaks have occurred historically on the Kenai Peninsula, the magnitude of the recent infestation distinguished it from previous events (Berg et al., 2006).

Several factors are known to influence spruce beetle population levels. Beetles maintain a constant presence in spruce forests but can exceed endemic levels when environmental conditions are favorable. Disturbances such as fire, large wind-throw events, or timber harvest can result in population growth when sufficient numbers of injured or newly killed spruce remains on site (Furniss and Carolin, 1977). Recent studies from the Kenai Peninsula suggest that localized outbreaks can reach epidemic levels when there is an uninterrupted succession of warm summers. These population

* Corresponding author at: Alaska Natural Heritage Program, University of Alaska Anchorage, 707 A Street, Anchorage, AK 99501, USA.
Tel.: +1 907 257 2784; fax: +1 907 257 2789.

E-mail address: antvb@uaa.alaska.edu (T.V. Boucher).

growth episodes have historically occurred every 50 years in the region and have ended following cool, moist summers. Since 1987, the Kenai Peninsula experienced an unprecedented run of above-average summer temperatures, allowing spruce beetle populations to expand until a shortage of host trees forced their decline (Berg et al., 2006). Other spruce beetle outbreaks occurred over extensive areas in interior Alaska and Canada's Yukon Territory during this same time period and raised concerns of a broader warming trend and related changes to the disturbance regime.

The effects of spruce beetle outbreaks on forest plant communities depend largely on site conditions, initial forest composition, and the severity of the infestation. Of particular concern is the grass bluejoint which increases in abundance following overstory tree removal and can inhibit forest regeneration when abundant by lowering recruitment and growth of tree seedlings (Eis, 1981; Powelson and Lieffers, 1992). A study from the Resurrection Creek valley in the Kenai Mountains found that bluejoint and fireweed abundance increased in cover and plant species diversity decreased from 1980 to 1991 following both spruce beetle infestation and prescribed fire (Holsten et al., 1995). However, a more broadscale evaluation of plant community responses is needed to determine if such changes occur widely among infested forests of the Kenai Peninsula, which encompass a far wider range of site conditions than represented in the Resurrection Creek study.

In 1987, the U.S. Forest Service, Pacific Northwest Research Station, Forest Inventory and Analysis Program conducted initial and in 2000 remeasurement inventories of forest vegetation to assess the impacts of the recent spruce beetle infestation on forests of the Kenai Peninsula. van Hees (2005) previously assessed reproduction dynamics of Sitka and white spruce across the study area using these data and found no significant changes in regeneration between 1987 and 2000, although the degree of beetle-induced mortality varied across the Kenai Peninsula. In this study, we assess the direction and degree of compositional change in vegetation resulting from the spruce beetle infestation and whether such changes vary among geographic regions on the Kenai Peninsula. We also evaluate spruce and paper birch seedling recruitment given different understory conditions, including the response of bluejoint to spruce mortality, and its impact on seedling recruitment.

2. Materials and methods

2.1. Study area

This study was conducted on Alaska's Kenai Peninsula, between 148°30' and 152°00' west longitude and 59°05' and 61°05' north latitude (Fig. 1). The Kenai Peninsula is a geologically and ecologically diverse area of 2.1 million ha, of which 772,000 ha can support forest (van Hees and Larson, 1991). Vegetation cover and disturbance dynamics varies across the three ecologically distinct regions: Cook Inlet Basin, Chugach-St. Elias Mountains, and the Gulf of Alaska Coast (Nowacki et al., 2001). In this paper these regions are respectively referred to by their local landforms: Kenai

Lowland, Kenai Mountains, and Gulf Coast (Fig. 1). The forests of the Kenai Peninsula range from coastal temperate rain forests dominated by Sitka spruce and mountain hemlock along the Gulf Coast, to the boreal forests of white spruce-paper birch and black spruce (*Picea mariana*) on the Kenai Lowland. Where the ranges of Sitka and white spruce overlap, they cross-pollinate to produce the hybrid Lutz spruce (*Picea × lutzii*). Because of the difficulty in consistently distinguishing Lutz spruce from white or Sitka spruce based on field characteristics, a geographic boundary was used to assign Lutz spruce to either Sitka or white spruce. Lutz spruce in the Gulf Coast was referred to as Sitka spruce, and Lutz spruce in the Kenai Mountains and Kenai Lowland was referred to as white spruce.

The Kenai Lowland is characterized by level to rolling surfaces in the north and low hills in the south. The entire region is covered with a loess mantle and discontinuous ash layers (Karlstrom, 1964). Owing to the distinct differences in topography and climate across the Kenai Lowland, the region was further divided into the northern and southern Kenai Lowland subregions separated by Tustumena Lake to better describe vegetation changes after beetle-induced tree mortality.

The topography of the northern Kenai Lowland is flat to gently rolling and features moraines, ancient lakebeds, poorly integrated drainages, and numerous small lakes (Karlstrom, 1964). Black spruce muskeg is common on poorly drained flats, whereas forests of paper birch, white spruce, and quaking aspen (*Populus tremuloides*) are common on upland areas. The southern Kenai Lowland is dominated by the Caribou Hills, a series of upland plateaus that rises south of Tustumena Lake to an elevation of 785 m. In contrast to the northern Kenai Lowland, the southern Kenai Lowland features well-defined drainages, higher elevations, and continuous forests of mature white spruce in addition to mixed forests of white spruce-paper birch. Average annual precipitation decreases across the region from the southern (750–800 mm) to northern Kenai Lowland (450–500 mm; Daly, 2002). The Caribou Hills hold snow until relatively late in the growing season, which, combined with dense soils and abundant summer rainfall, maintains a water table near the surface. Bluejoint is a common understory grass occurring on sites with deep moist soil.

The Kenai Mountains, together with the Chugach and St. Elias Mountains, form a crescent shaped barrier adjacent to the Gulf Coast region. The entire range is heavily glaciated, and the topography is characterized by rugged peaks and U-shaped valleys. The Harding Icefield dominates the southern portion of the Kenai Mountains. Soils, in areas not covered by glaciers or permanent snowfields, developed from glacial till and colluvium. Spruce and hardwood forests occur in the lower elevations and along rivers, and mountain hemlock is common at higher elevations (McNab and Avers, 1994). Average annual precipitation increases with elevation from 650 to 2400 mm on the lower slopes to 3000–4000 mm on the Harding Icefield (Daly, 2002).

The Gulf of Alaska Coast region is characterized by a narrow band of rugged terrain along the coast, which extends from the southern tip of the Kenai Peninsula east along the coast to the Fairweather Range south of Yakutat. Climate in this region is maritime-influenced with heavy rainfall (1200–4000 mm

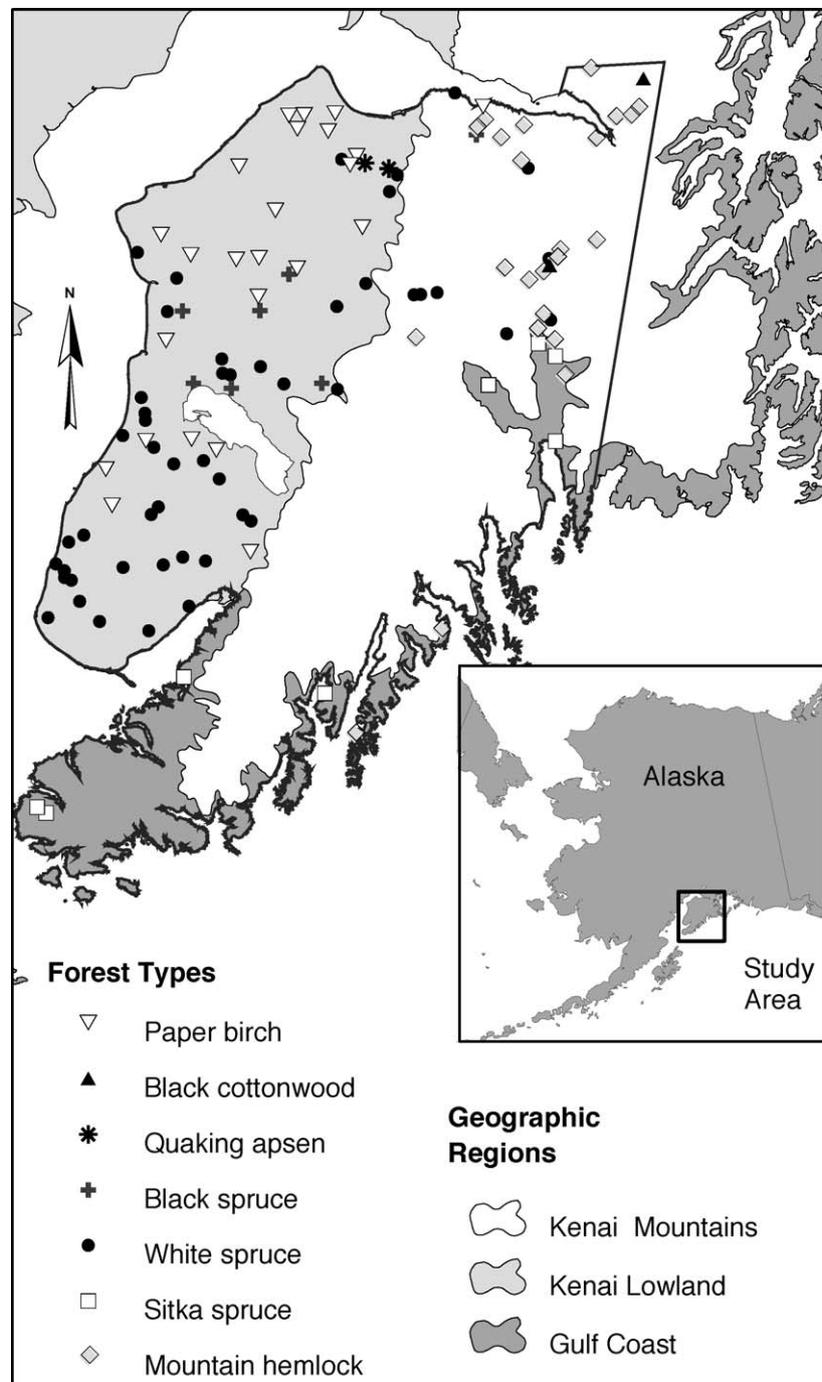


Fig. 1. The location, geographic region, and forest type of 115 vegetation plots sampled on the Kenai Peninsula, Alaska, 1987–2000. Tustumena Lake separated the northern and southern portions of the Kenai Lowland.

annually) and moderate temperatures. Elevation rises from sea level to over 1000 m. The Kenai portion of the Gulf Coast features mountain hemlock and Sitka spruce forests (McNab and Avers, 1994).

2.2. Vegetation sampling

For the 1987 inventory, 5597 photopoints were systematically distributed and interpreted over 1:60,000 scale aerial photographs using a 0.4 ha minimum area for classification. From

these a random draw of 130 photopoints (plots hereinafter) on productive forest lands was selected for vegetation measurement. Productive forest lands were: (1) at least 10% stocked with live trees of any size, or formerly had such tree stocking and were not currently developed for nonforest use, and (2) capable of producing $\geq 1.4 \text{ m}^3$ of industrial wood per ha per year at the culmination of mean annual increment (MAI). Plot vegetation was sampled using a cluster of five subplots that included one central subplot and four subplots located 100 m in each cardinal direction. From the 130 plots measured in 1987, 115 could be

precisely located and remeasured in 2000 and formed the basis for analyses. Fifteen plots could not be relocated due to inadequate monumentation or development. Substitute plots were measured but were not used in analyses of vegetation dynamics. Detailed data collection procedures are described by U.S. Forest Service (1987, 2000).

Variable-radius sampling with a metric basal area factor of 4 was used to select a sample of trees >10 cm in diameter at breast height (dbh) at each subplot. Measurements taken on these trees were used to estimate plot foliar cover, stand-size class, forest type, volume, and site productivity. Although many stands featured a mix of tree species in the overstory, a single-species forest type was assigned to each plot based on the species with the greatest stocking. Established tree seedlings (trees < 2.5 cm dbh) and saplings (trees 2.5–9.9 cm dbh) were counted within 1.5-m fixed-radius microplots centered on each subplot. A seedling was considered established if it had good coloration, no evidence of disease, and a root system in contact with mineral soil. Each plot was assigned to a stocking class in 1987 and 2000 based on the average size class of live trees. A plot was considered stocked if it had $\geq 10\%$ cover of live trees or ≥ 5 established tree seedlings.

Site productivity was measured by taking the age and heights of trees to determine species site index, the maximum height attained at rotation age (120 years for spruce), and site productivity class as determined by the culmination of MAI (Taylor, 1934; Gregory and Haack, 1965; Farr, 1967). Trees selected to determine site index were free-growing and dominant or codominant in the canopy. Trees were cored using an increment borer and aged by counting growth rings. When growth rings could not be seen clearly in the field, cores were counted using a dissecting scope in the office. A mean site index for each plot was determined by averaging the height and age of site trees at or below 120 years. Stand age was determined by taking cores from three trees on or near the plot representing the average age of the stand.

To determine site productivity, each site tree was plotted based on its age and height along MAI curves for each species and plot. A table correlating site index and site productivity class was not available for the Kenai Peninsula, so site index curves developed for other parts of Alaska or other species were used to calculate site productivity for white spruce (Farr, 1967), paper birch (Gregory and Haack, 1965), and mountain hemlock (Taylor, 1934). In some cases a single tree skewed the potential MAI toward low values. These outlier trees were dropped and the site was assigned a higher productivity class. In other cases, a single off-plot site-index tree was determined to have arbitrarily raised the site productivity class above a level indicated by the age and height of other trees on the plot, so productivity class was lowered one class. This was an attempt to evaluate all the evidence and make the best judgment as to actual productivity potential of the site.

Vegetation cover was measured in natural layers for tree seedlings (dbh < 2.5 cm) and plants other than trees and saplings on 5.64-m radius microplots centered on the first two subplots typical of the overall vegetation type of the plot. Typical layers defined were tall and low shrubs, herbaceous and subshrubs, and

ground-cover vegetation with the lowest and tallest height for each layer recorded on each microplot. For each microplot and layer, vegetative cover and the percentage of vegetative cover occupied by each individual species were visually estimated. The product of these two measures was used to compute percent cover by species and layer with the greatest cover value among layers for a species used to estimate its cover for the microplot. A species' cover was then averaged between the two microplots to estimate its cover for the vegetation plot. Number of species per plot determined species richness. Percent slope for each plot was based on the average slope of the two vegetation subplots.

Crown area, computed using crown radius measurements, was used to estimate cover for saplings (2.5–9.9 cm dbh). Trees greater than 10 cm dbh were measured on variable plots; these trees had a corresponding variable-plot radius computed by multiplying their dbh (cm) by 0.25, the corresponding limiting distance factor. Each tree's crown area was then divided by its plot area and the result multiplied by 100, to compute a percentage of crown cover per tree. Tree crown covers were then summed by species for each plot. Tree cover was computed only for the two subplots with corresponding vegetation profiles measured.

Average annual precipitation for each plot was taken from a precipitation model for the Kenai Peninsula that was based on a 29 year average (1961–1990) of precipitation data from local weather stations (Daly, 2002).

2.3. Analysis methods

Basal area was computed for each tree species measured on each plot (tree count \times basal area factor/five subplots) and then averaged by species among plots for each region. Basal area for 1987 included spruce that died up to 5 years prior to 1987 to capture trees that succumbed to spruce beetles in the early years of the outbreak.

Changes in plant composition were evaluated using nonmetric multidimensional scaling (NMS), a nonparametric ordination technique that uses ranked distances to position plots in species space and avoids assumptions of linear relationships among variables (McCune and Grace, 2002). Species that occurred on fewer than three plots were not included in the analysis. The final data set consisted of 91 species and 230 plots (115 plot-pairs) for the Kenai Peninsula and 74 species and 144 plots (72 plot-pairs) for the Kenai Lowland subset. To equalize the importance of common and uncommon species, the values for each species were standardized relative to the maximum value for each plot. Sørensen dissimilarity was used to calculate the distance matrix for the ordination. Random starting configurations and 40 runs with real data were used to compute the ordination solution with the dimensionality of each data set assessed by requesting a step-down from a six-dimensional ordination. A three-dimensional solution was selected. The strength of the resulting ordination was evaluated using a Monte Carlo test that compared the final axes to axes calculated from 50 runs of randomized data.

Graphs of sample plots in ordination space with overlays of environmental variables were used to describe the ordination gradients and how they varied by region and forest type. Vectors

linking 1987 and 2000 measurements were used to display direction of change for each plot. The environmental gradients represented by the ordination axes were further described by using Pearson correlations to test for significant relationships between each ordination axis and each environmental or plant species variable. The significance of correlations was based on sample size following Zar (1984).

Differences in the direction of vectors of vegetation change among regions was examined by: (1) standardizing each plot vector to a common origin by subtracting the 1987 plot ordination score from both ends of the plot vector of vegetation change (1987–2000 measurement) and (2) using a multiresponse permutation procedure (MRPP) with Euclidean distance to test whether the direction of compositional change varied among regions. MRPP is a multivariate nonparametric technique used to test the hypothesis that there is no difference between two or more groups (McCune and Mefford, 1999; McCune and Grace, 2002). The effect size (A) describes the chance-corrected within-group agreement. When all items are identical within groups $A = 1$; when within-group heterogeneity equals that expected by chance $A = 0$. When differences between groups are greater than expected by chance $A > 0$. Vector length, a measure of the magnitude of vegetation change between 1987 and 2000, was calculated for each plot in three-dimensional space using the plot ordination scores for each of the axis. One-way analysis of variance (ANOVA) was used to test for an overall difference in mean vector length among geographic regions; Tukey–Kramer multiple comparisons were used to test for specific differences between regions (SAS Institute, 1999).

To evaluate broad trends across the study area, vegetation change was initially assessed by analyzing all 115 vegetation plots together. The subset of 72 plots on the Kenai Lowland was then specifically examined because the effects of the spruce beetle were most extensive in this region, particularly in the southern Kenai Lowland (see Section 3). Additional analysis were not performed for the Kenai Mountains and Gulf Coast where the impact of the spruce beetle was less severe, and the pattern was adequately displayed in the ordination that included all plots (see Section 3).

Changes in species richness and the number of white spruce and paper birch seedlings between 1987 and 2000 were assessed using paired t -tests (SAS Institute, 1999). The impact of bluejoint expansion on species richness was evaluated by comparing the number of plant species observed in 1987–2000 on plots that showed $\geq 10\%$ increase in bluejoint cover.

3. Results

3.1. Kenai Peninsula

3.1.1. Changes in basal area and stocking

Levels of spruce beetle-induced mortality differed across the Kenai Peninsula. Spruce mortality from 1987 to 2000 was most extensive in mature spruce forests of the southern Kenai Lowland but less severe in the northern Kenai Lowland and Kenai Mountains where spruce is often a secondary overstory species (Table 1). On the southern Kenai Lowland basal area of

Table 1
Average basal area \pm S.E. (number of plots on which a tree species occurred) of live trees > 12.7 cm dbh by geographic region (number of plots sampled) and year on 115 vegetation plots measured on the Kenai Peninsula, Alaska, 1987 and 2000

Tree species ^a	Kenai Mountains (24)		Gulf Coast (19)		Northern Kenai Lowland (39)		Southern Kenai Lowland (33)	
	1987	2000	1987	2000	1987	2000	1987	2000
Hemlock	8.2 \pm 1.8 (16)	10.2 \pm 2.0 (16)	15.6 \pm 3.6 (12)	16.7 \pm 3.9 (12)	<0.1 \pm <0.1 (1)	<0.1 \pm <0.1 (1)	–	–
White spruce	15.6 \pm 2.1 (24)	8.4 \pm 1.6 (24)	–	–	8.7 \pm 0.9 (35)	6.3 \pm 0.7 (35)	22.7 \pm 1.6 (33)	2.9 \pm 1.0 (23)
Black spruce	<0.1 \pm <0.1 (1)	0.1 \pm 0.1 (1)	–	–	0.6 \pm <0.1 (10)	0.5 \pm 0.1 (12)	0.3 \pm 0.2 (4)	0.1 \pm 0.1 (3)
Sitka spruce	–	–	19.4 \pm 3.7 (19)	15.2 \pm 3.1 (19)	–	–	–	–
Paper birch	2.2 \pm 0.9 (13)	2.3 \pm 1.0 (13)	–	–	6.7 \pm 1.0 (29)	6.1 \pm 1.0 (29)	3.5 \pm 0.7 (24)	2.7 \pm <0.6 (22)
Black cottonwood	0.5 \pm 0.3 (6)	0.8 \pm 0.4 (6)	1.3 \pm 1.2 (2)	1.6 \pm 1.5 (2)	0.1 \pm <0.1 (3)	0.1 \pm <0.1 (4)	–	–
Quaking aspen	0.4 \pm 0.4 (1)	0.4 \pm 0.4 (1)	–	–	2.4 \pm 0.6 (18)	2.2 \pm 0.5 (18)	0.2 \pm 0.1 (5)	0.2 \pm 0.1 (5)
Total	27.0 \pm 2.3 (24)	22.3 \pm 2.3 (24)	36.3 \pm 2.8 (19)	33.4 \pm 3.3 (19)	18.6 \pm 1.3 (38)	15.2 \pm 1.4 (38)	26.8 \pm 1.4 (33)	5.9 \pm 1.2 (27)

^a Hemlock = mountain hemlock.

white spruce >12.7 cm dbh decreased by 87%, whereas basal area of white spruce in the Kenai Mountains decreased by 46%. Forests of the Gulf Coast and northern Kenai Lowland had lower levels of spruce mortality (22% reduction of Sitka spruce and 28% reduction of white spruce, respectively). Sitka spruce along the Gulf Coast were killed by spruce beetles only along the western edge of the region. In the southern Kenai Lowland 76% of the plots shifted from stocked to nonstocked. In the Kenai Mountains, Gulf Coast, and northern Kenai Lowland, changes in stand structure were less dramatic, with 8, 11, and 10% of plots shifting from stocked to nonstocked, respectively.

3.1.2. Ordination

For the final three-dimensional ordination, model stress was 15.92 and instability was <0.0001. The axes extracted were stronger than those expected by chance ($P = 0.02$) based on the Monte Carlo test. The first three axes explained 76% of the variance in the data with 65% of the variation explained by axes 1 (27%) and 3 (38%). Overall, the gradients captures in axes 1 and 3 showed a strong association between forest type and

region (Fig. 2). Plots in the southern Kenai Lowland were dominated by white spruce, the northern Kenai Lowland plots featured paper birch and black spruce, and plots in Kenai Mountains featured a mix of mountain hemlock and spruce (Figs. 1 and 2). Species correlated with axis 1 indicated a gradient in plant succession; late successional species were negatively correlated and early successional species were positively correlated with axis 1. Species correlations with axis 3 showed a gradient in site productivity. Species associated with high and low site productivity were positively and negatively correlated with axis 3, respectively (Table 2). Several of the most highly correlated species showed differences in cover in particular regions between 1987 and 2000 (Table 3).

Along axis 1, plots were distributed according to region and related differences in climate, topography, and changes in vegetation composition resulting from spruce beetles infestations (Fig. 2). Precipitation and slope were negatively correlated with axis 1 and were related to a gradient from the maritime Gulf Coast (high precipitation and steep slopes;

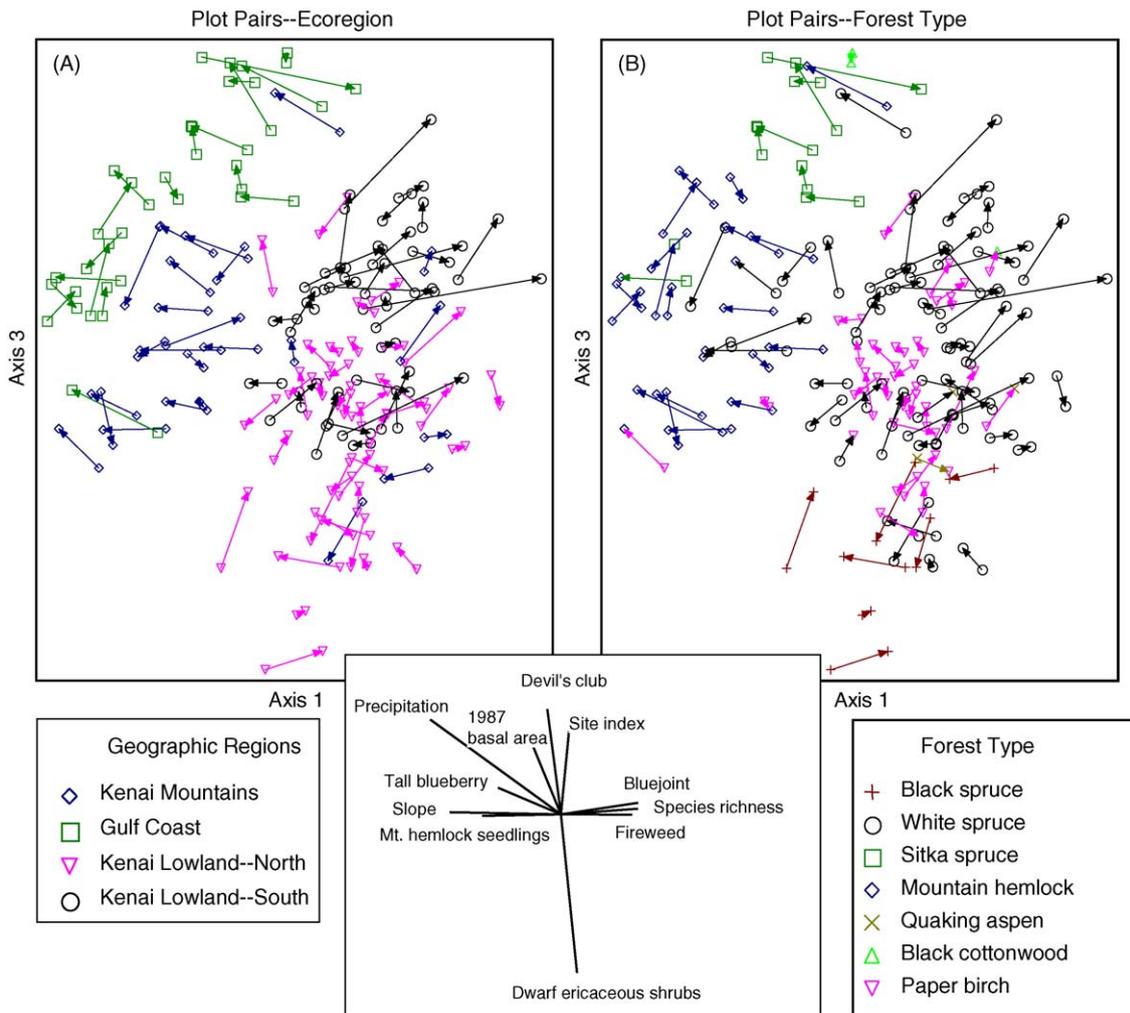


Fig. 2. Nonmetric multidimensional scaling diagrams of 115 vegetation plots across the Kenai Peninsula, Alaska. Each plot was sampled in 1987 and 2000 with the direction and magnitude of vegetation change between years for each plot indicated by a directional vector. Vegetation plots are represented by: (A) geographic region and (B) forest type. Vectors in the inset show the direction and strength of correlation of variables with the ordination axes. Axis 1 represented a climatic and geographic gradient from the maritime Gulf Coast (left) to the more interior climate of the Kenai Lowland (right). Axis 3 represented a gradient in site productivity.

Table 2

Correlation coefficients (r) between ordination axes and plant cover for the 30 plant species variables most strongly correlated with axes 1 and 3, Kenai Peninsula, Alaska (15 most positively correlated and 15 most negatively correlated)

Axis 1	r	Axis 3	r
Mountain hemlock (tree)	-0.76	Lowbush cranberry	-0.66
Mountain hemlock (seedling)	-0.48	Black spruce (seedling)	-0.42
Mountain hemlock (sapling)	-0.47	Northern commandra	-0.41
Tall blueberry	-0.44	Black spruce (sapling)	-0.39
Rusty menziesia	-0.35	Crowberry	-0.38
Sitka spruce (seedling)	-0.31	Quaking aspen (seedling)	-0.35
Beach fern	-0.29	Bunchberry	-0.32
Sitka spruce (tree)	-0.27	White spruce (seedling)	-0.31
Devil's club	-0.21	Prickly rose	-0.29
Salmonberry	-0.20	Black spruce (tree)	-0.26
Three-leaved goldthread	-0.20	Twin flower	-0.25
Foam flower	-0.18	Bog blueberry	-0.25
Alpine heuchera	-0.17	Quaking aspen (tree)	-0.23
Goat's beard	-0.13	Paper birch (tree)	-0.23
Mountain ash	-0.10	Labrador tea	-0.23
Paper birch (seedling)	0.24	Currant	0.22
Sidebells	0.24	Black cottonwood (tree)	0.23
Liverleaf wintergreen	0.24	Tall blueberry	0.28
Twisted stalk	0.26	Oak fern	0.29
Nagoon berry	0.27	Sitka spruce (seedling)	0.32
Jacob's ladder	0.27	Foam flower	0.33
Willow (<i>Salix</i> sp.)	0.29	Lady fern	0.35
Currant	0.29	Twisted stalk	0.35
Northern geranium	0.32	Sweet bedstraw	0.35
Prickly rose	0.32	Red elderberry	0.41
Star flower	0.34	Sitka alder	0.42
Sitka burnet	0.36	Five-leaf bramble	0.43
Twin flower	0.36	Sitka spruce (tree)	0.44
Fireweed	0.47	Shield fern	0.51
Bluejoint	0.49	Devil's club	0.57

Scientific names of plants are in Appendix A; $r > 0.13$ and $r < -0.13$ were at $\alpha < 0.05$ for a sample size of 230 plots (Zar, 1984).

low axis values) to the more interior climate of the Kenai Lowlands (low precipitation and gentle slopes; high axis values). The Kenai Mountains occupied an intermediate position along axis 1 between these maritime and interior climates, and had variable precipitation and slopes (Fig. 2 and Table 4).

Table 3

Average cover \pm S.E. (number of plots with species) by region (number of plots in region) and year for species that were highly correlated with ordination axis 1, Kenai Peninsula, Alaska

Plant species ^a	Kenai Mountains (24)		Gulf Coast (19)		Northern Kenai Lowland (38)		Southern Kenai Lowland (33)	
	1987	2000	1987	2000	1987	2000	1987	2000
Hemlock, tree	21.0 \pm 5.3 (16)	39.1 \pm 7.6 (16)	28.6 \pm 7.2 (12)	35.7 \pm 9.2 (12)	0.1 \pm 0.1 (1)	0.2 \pm 0.2 (1)	–	–
Hemlock, seedling	6.7 \pm 1.7 (16)	3.5 \pm 1.1 (17)	4.1 \pm 1.4 (11)	2.1 \pm 0.7 (11)	<0.1 \pm <0.1 (1)	<0.1 \pm <0.1 (1)	–	–
Hemlock, sapling	6.9 \pm 2.3 (9)	13.0 \pm 4.2 (8)	8.4 \pm 3.7 (5)	2.0 \pm 1.4 (2)	–	–	–	–
Tall blueberry	1.8 \pm 0.7 (15)	1.7 \pm 0.9 (12)	11.0 \pm 3.5 (17)	15.2 \pm 3.8 (16)	0.3 \pm 0.2 (7)	0.2 \pm 0.1 (7)	1.0 \pm 0.3 (12)	0.6 \pm 0.2 (11)
Rusty menziesia	9.5 \pm 1.9 (18)	8.3 \pm 1.7 (18)	7.5 \pm 1.8 (15)	7.2 \pm 1.8 (15)	8.5 \pm 2.6 (15)	10.2 \pm 3.1 (15)	9.1 \pm 2.9 (13)	5.1 \pm 2.0 (13)
Sitka burnet	0.4 \pm 0.2 (7)	0.3 \pm 0.1 (7)	0.1 \pm 0.1 (2)	0.1 \pm 0.1 (1)	0.9 \pm 0.4 (9)	0.4 \pm <0.2 (8)	3.3 \pm 0.8 (21)	2.3 \pm 0.4 (22)
Twin flower	2.4 \pm 0.6 (19)	1.2 \pm 0.5 (17)	0.3 \pm 0.2 (6)	0.1 \pm 0.1 (4)	5.9 \pm 0.8 (37)	4.3 \pm 0.8 (34)	5.1 \pm 0.7 (30)	4.9 \pm 1.0 (29)
Fireweed	0.6 \pm 0.2 (12)	0.6 \pm 0.2 (11)	0.1 \pm 0.1 (2)	0.1 \pm 0.1 (2)	2.0 \pm 0.3 (36)	2.2 \pm 0.6 (35)	2.2 \pm 0.4 (30)	4.3 \pm 0.8 (32)
Bluejoint	1.1 \pm 0.6 (15)	0.8 \pm 0.3 (11)	0.9 \pm 0.3 (9)	0.3 \pm 0.1 (8)	3.7 \pm 1.3 (27)	4.6 \pm 1.3 (26)	5.2 \pm 0.7 (31)	13.7 \pm 2.1 (33)

^a Hemlock = mountain hemlock.

Table 4

Correlation coefficients (r) between ordination axes and environmental variables, seedling counts, and combined species variables Kenai Peninsula, Alaska

Axis 1	r	Axis 3	r
Precipitation	-0.71	Dwarf ericaceous shrubs	-0.70
Average slope	-0.59	Black spruce seedlings	-0.40
Mountain hemlock seedlings	-0.47	Quaking aspen seedlings	-0.32
Softwood seedlings	-0.34	Hardwood seedlings	-0.32
		White spruce seedlings	-0.30
		Softwood seedlings	-0.24
		Paper birch seedlings	-0.23
Paper birch seedlings	0.21		
Dwarf ericaceous shrubs	0.22	Sitka spruce seedlings	0.25
Hardwood seedlings	0.27	Precipitation	0.46
Species richness	0.49	Site index	0.50

Only variables with $r > 0.2$ or $r < -0.2$ are listed.

Axis 1 also showed divergent trends in the length and direction of vectors linking 1987 and 2000 vegetation measurements of each plot (Fig. 2), both measures of vegetation composition change resulting from spruce beetle infestations. Between 1987 and 2000, plots in the southern Kenai Lowland shifted toward earlier successional species (high axis values), whereas plots in the Kenai Mountains shifted toward later successional species (low axis values). Bluejoint and fireweed cover had the strongest positive correlations with axis 1 (Table 2); plots that showed increases of $\geq 10\%$ in cover of either species were largely restricted to the southern Kenai Lowland (14 of 15 plots). The average cover of bluejoint and fireweed increased by 163% and 95%, respectively from 1987 to 2000 in this subregion (Table 3). Mountain hemlock and tall blueberry (*Vaccinium ovalifolium*) cover had the strongest negative correlations with axis 1; plots that showed increases of $\geq 10\%$ in cover of either species occurred mostly within the Kenai Mountains (15 out of 17 plots). Average cover of mountain hemlock trees and saplings approximately doubled from 1987 to 2000, however, average cover of mountain hemlock seedlings was reduced by 48% and average cover of tall blueberry did not change in this region (Table 3).

Axis 3 was positively correlated with site index, indicating that plots with higher scores along the axis were on more productive sites. Species whose cover was correlated with axis

3 also indicated a productivity gradient. Devil's club (*Oplopanax horridus*), an indicator of highly productive forest types (DeMeo et al., 1992), had a strong positive correlation with the axis, while dwarf ericaceous shrubs, which typically indicate low site productivity (Holloway, 1981; Korcak, 1988; Klinka et al., 1989; Henry et al., 1990), were negatively correlated with axis 3 (Fig. 2 inset and Table 4). Included in dwarf ericaceous shrubs were lowbush cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), bog blueberry (*V. uliginosum*), and Labrador tea (*Ledum palustre* and *L. groenlandicum*).

Species richness in 2000 averaged 20.5 species per plot, ranged from 9 to 37 species, and was positively correlated with axis 1 (Fig. 2 inset and Table 4). There was no clear relationship between bluejoint expansion and species richness. There were ≥ 20 species per plot on all plots where bluejoint expanded by $\geq 10\%$ in cover and species richness did not change on these plots between 1987 and 2000 ($t = -1.2$, d.f. = 11, $P = 0.24$).

Seedlings of white spruce, black spruce, and quaking aspen were associated with less productive sites, whereas Sitka spruce seedlings were associated with more productive sites (Table 4). With few exceptions, seedling numbers did not change dramatically between 1987 and 2000. In 2000, 29 plots (25%) had 1–4 seedlings of any species and 65 plots (57%) had at least 5 seedlings. Of the 21 plots (18%) with no seedlings of any species, 12 plots were not stocked with overstory trees.

3.1.3. Vector analysis

The direction of change from 1987 to 2000 in plant composition differed among geographic regions (MRPP; $A = 0.06$, $P < 0.0001$). Specifically, the direction of change between the Kenai Mountains and the southern portion of the Kenai Lowland differed (MRPP; $A = 0.12$, $P < 0.0001$). The direction of change did not differ significantly among the other geographic regions (Fig. 3). Vectors linking 1987–2000 vegetation measurements for each plot also varied in mean length by geographic

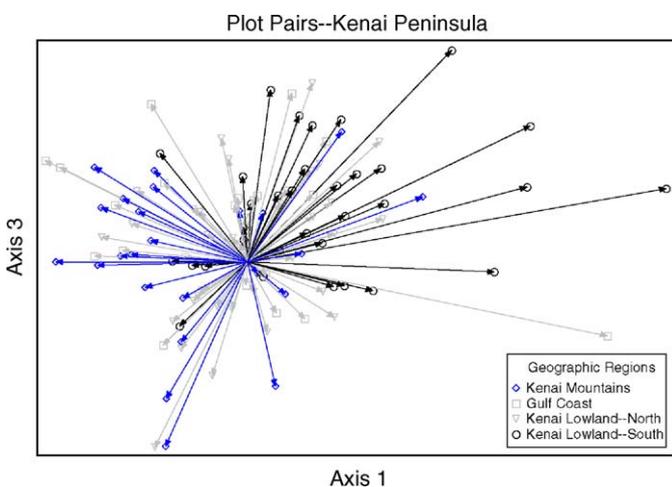


Fig. 3. Nonmetric multidimensional scaling diagram of vegetation change (1987–2000) for 115 vegetation plots across the Kenai Peninsula, Alaska. The 1987 ordination scores were translated to a common origin among vegetation plots with the direction and magnitude of vegetation change between years for a plot indicated by a directional vector. Plots in the Kenai Mountains generally had lower scores along axis 1 in 2000 compared to 1987. Plots in the southern Kenai Lowland had higher scores in 2000 compared to 1987.

region ($F = 3.6$, d.f. = 3, $P = 0.02$; Fig. 3). The mean vector length of plots in the northern Kenai Lowland (0.27 ± 0.02) was less than mean vector length of plots in the Kenai Mountains (0.40 ± 0.04) and southern Kenai Lowland (0.38 ± 0.04 , $P < 0.05$). The mean vector length of Gulf Coast plots (0.32 ± 0.04) was not significantly different from those of other regions.

3.2. Kenai Lowland

3.2.1. Ordination

For the final ordination specific to the Kenai Lowlands, model instability was < 0.0001 , and stress was 16.49. The axes extracted were stronger than those expected by chance ($P = 0.02$) based on the Monte Carlo test. The first three axes explained 76% of the variance among plots; 52% of the variance was explained by axes 1 (28%) and 3 (24%). The ordination was rotated 270° so that the axes matched the ordination that included all plots sampled on the Kenai Peninsula. The gradients and vegetation trends associated with this ordination were similar to those displayed in the previous ordination. However, because the Kenai Lowland vegetation was more homogeneous than vegetation across the entire Kenai Peninsula, the climatic and geographic gradients were less pronounced among the Kenai Lowland plots and a more distinct disturbance signature was revealed (Fig. 4).

Subregion separated plots along axis 1, with northern Kenai Lowland plots generally having low values and southern Kenai Lowland plots having high values (Fig. 4). Axis 1 also showed the effect of disturbance on species composition with the vectors of vegetation change linking plot pairs (1987 and 2000) longest in the southern Kenai Lowland (Fig. 4); the area with the most severe spruce mortality. Bluejoint, Sitka burnet (*Sanguisorba canadensis*), twisted stalk (*Streptopus amplexifolius*), geranium (*Geranium erianthum*), and fireweed had strong positive correlations with axis 1, whereas lowbush cranberry, paper birch, prickly rose (*Rosa acicularis*), bunchberry (*Cornus canadensis*), and northern commandra (*Geocaulon lividum*) had strong negative correlations with axis 1. Site index and pre-outbreak basal area were positively correlated with both axes 1 and 3 (Fig. 4 and Table 5).

Along axis 3, plots were again arranged according to a gradient in site productivity (Table 6). Black spruce and dwarf ericaceous shrubs, such as lowbush cranberry, crowberry, and bog blueberry, were negatively correlated with axis 3; whereas site productivity, Sitka alder (*Alnus viridis* ssp. *sinuata*) shield fern (*Dryopteris expansa*), and devil's club were positively correlated with axis 3 (Fig. 4 and Table 5).

3.2.2. Forest regeneration

Densities of white spruce seedlings on the Kenai Lowland did not change from 1987 to 2000 ($t = 0.76$, d.f. = 71, $P = 0.45$). Plots with higher numbers of spruce seedlings tended to occur on low-productivity sites (Fig. 5d and e). The one exception to this was plot 95 in the southern Kenai Lowland (Fig. 5d). This plot fell in a developed residential area near a road, was partially harvested, did not experience rapid bluejoint expansion, and had a high seedling count for white spruce on one subplot in 2000. Although paper birch seedlings occurred in the

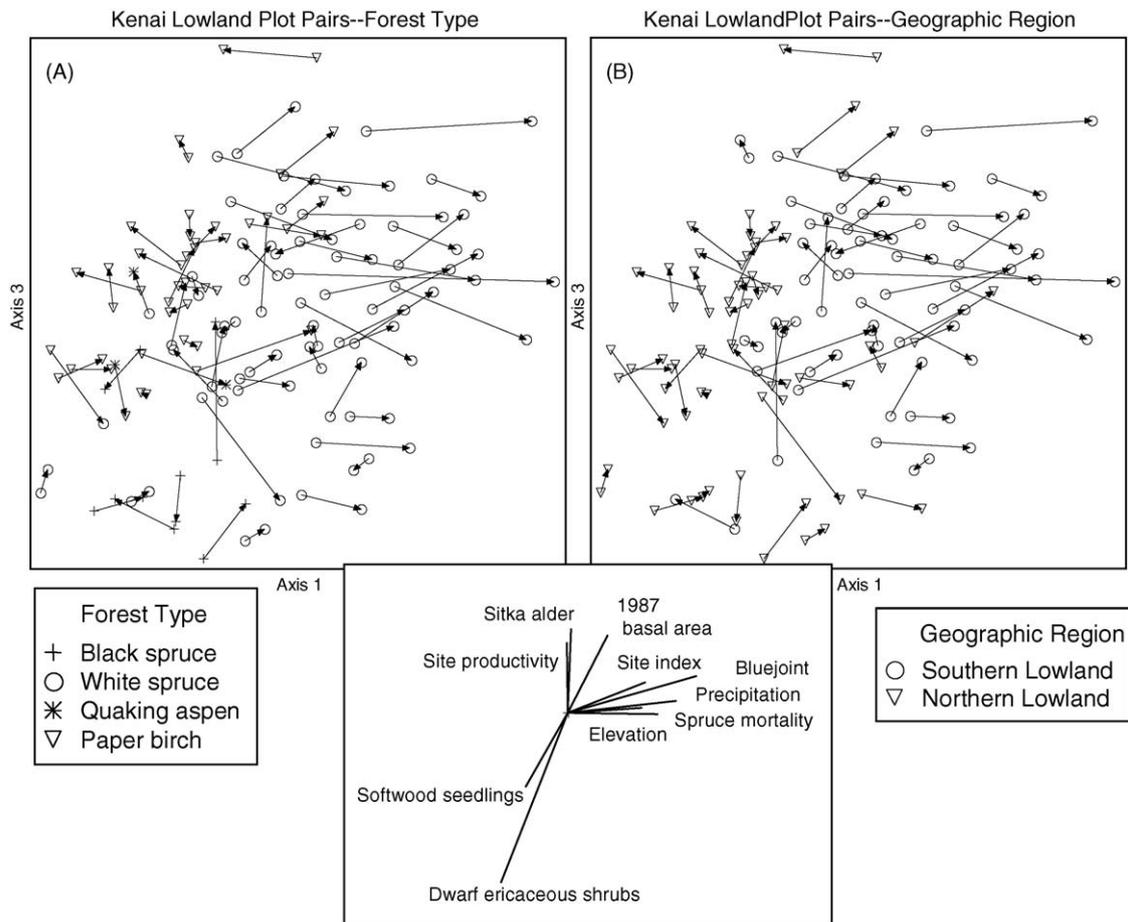


Fig. 4. Nonmetric multidimensional scaling diagrams of 72 vegetation plots across the Kenai Lowland, Kenai Peninsula, Alaska. Each plot was sampled in 1987 and 2000 with the direction and magnitude of vegetation change between years for a plot indicated by a directional vector. Vegetation plots are represented by: (A) forest type and (B) geographic region. Vectors in the inset show the direction and strength of correlation of variables with the ordination axes. Axis 1 represented a gradient in disturbance and geographic location. Axis 3 represented a gradient in site productivity.

highest numbers in the birch forest type, they also occurred across all forest types and their abundance was not correlated with ordination axis 1 or 3 (Fig. 5c). Paper birch seedling abundance increased marginally between 1987 and 2000 on the Kenai Lowland ($t = -1.65$, d.f. = 71, $P = 0.10$).

Table 5
Correlation coefficients (r) between ordination axes and environmental variables and seedling counts on the Kenai Lowland region of the Kenai Peninsula, Alaska

Axis 1	r	Axis 3	r
Total seedlings	-0.35	Total seedlings	-0.46
Softwood seedlings	-0.32	Softwood seedlings	-0.43
Aspen seedlings	-0.28	Black spruce seedlings	-0.36
Black spruce seedlings	-0.25	Aspen seedlings	-0.27
White spruce seedlings	-0.24	White spruce seedlings	-0.27
		Hardwood seedlings	-0.20
1987 Basal area	0.33	Vector length	0.25
Total spruce mortality	0.46	Site index	0.30
Site index	0.47	Stand age	0.33
Vector length	0.50	Site productivity	0.45
Elevation	0.51	1987 basal area	0.47
Precipitation	0.55		

Only variables with $r > 0.2$ or $r < -0.2$ are listed.

Bluejoint increased in cover by $\geq 10\%$ on 12 of the 33 plots in the southern Kenai Lowland, but did not increase at these levels elsewhere on the Kenai Peninsula. Six of these plots had no paper birch or white spruce seedlings counted in 1987 or 2000. Of the four plots that had white spruce seedlings, numbers were low (1–3 seedlings) and changed little from 1987 to 2000 (three increased and one decreased). Of the four plots that had paper birch seedlings, the numbers varied more widely; paper birch increased by 2 and 10 seedlings and decreased by 1 and 4 seedlings. Of the 25 plots on the southern Kenai Lowland that shifted from stocked to nonstocked, 14 had no spruce seedlings, 13 had no paper birch seedlings, and 8 had no seedlings of any tree species. Of the latter eight plots, three had $\geq 20\%$ cover of bluejoint in 2000.

4. Discussion

Changes in forest structure and vegetation composition in the aftermath of the spruce beetle outbreak on the Kenai Peninsula varied substantially by geographic region with divergent successional trends from 1987 to 2000 observed between forests of the Kenai Mountains and the southern Kenai Lowland. Forests in the Kenai Mountains tended to shift toward

Table 6
Correlations coefficients (r) between ordination axes and plant cover for the 30 plant species variables most strongly correlated with axes 1 and 3 on the Kenai Lowland region of the Kenai Peninsula, Alaska (15 most positively correlated and 15 most negatively correlated)

Axis 1	r	Axis 3	r
Lowbush cranberry	-0.61	Lowbush cranberry	-0.55
Paper birch (tree)	-0.51	Crowberry	-0.45
Prickly rose	-0.46	Black spruce (seedling)	-0.40
Bunchberry	-0.45	Black spruce (sapling)	-0.38
Northern commandra	-0.41	Bog blueberry	-0.37
Quaking aspen (tree)	-0.31	Northern commandra	-0.37
Highbush cranberry	-0.31	Willow	-0.35
Quaking aspen (seedling)	-0.26	Quaking aspen (seedling)	-0.34
Black spruce (seedling)	-0.26	Dwarf birch	-0.31
Black cottonwood (seedling)	-0.23	Black spruce (tree)	-0.31
Labrador tea	-0.23	Labrador tea	-0.29
Paper birch (sapling)	-0.21	White spruce (seedling)	-0.24
Lousewort	-0.20	Jacob's ladder	-0.20
Black spruce (sapling)	-0.19	Yarrow	-0.18
White spruce (seedling)	-0.19	Quaking aspen (tree)	-0.18
Willow	0.27	Paper birch (tree)	0.26
Woodland horsetail	0.28	Currant	0.27
Nagoon berry	0.28	Red raspberry	0.28
Common horsetail	0.29	Stiff clubmoss	0.29
Beauverd spiraea	0.29	Sweet bedstraw	0.29
False hellebore	0.30	Rusty menziesia	0.29
Monkshood	0.30	Twisted stalk	0.30
Currant	0.30	Star flower	0.32
Shield fern	0.32	Bluejoint	0.32
Five-leaf bramble	0.33	Devil's club	0.39
Fireweed	0.40	Red elderberry	0.41
Northern geranium	0.41	Five-leafed bramble	0.41
Twisted stalk	0.42	Oak fern	0.47
Sitka burnet	0.47	Shield fern	0.47
Bluejoint	0.61	Sitka alder	0.48

Scientific names are listed in Appendix A. $r > 0.17$ and $r < -0.17$ were at $\alpha < 0.05$ for a sample size of 144 plots (Zar, 1984).

later successional species while forests in the southern Kenai Lowland showed a dramatic shift toward early successional grasses and forbs. Forests on the Gulf Coast and northern Kenai Lowland, however, showed little directional change in vegetation composition. These regional patterns were related to initial forest composition which appeared to influence both the intensity of infestations and its effects on surviving vegetation.

The patchy spruce mortality (46% reduction in white spruce basal area) within the mountain hemlock-white spruce forests of the Kenai Mountains resulted in a transition in basal area dominance from white spruce in 1987 to late successional mountain hemlock in 2000. Furthermore, mountain hemlock trees and saplings nearly doubled in cover over this time period, accelerating a trend toward later successional forest composition. These patterns mirrored observations at the landscape level. Prior to the outbreak the two dominant forest types in the Kenai Mountains were mountain hemlock (30,000 ha) and mountain hemlock-spruce (25,000 ha). In 1999, after the infestation had declined, mountain hemlock had increased 22% in area to 36,500 ha and mountain hemlock-spruce decreased 28% in area to 18,000 ha (U.S. Forest Service, 2002).

This trend in succession was similar to that found among mixed-conifer subalpine forests in Colorado which shifted in dominance from Engelmann spruce (*Picea engelmannii*) to subalpine fir (*Abies lasiocarpa*) following a spruce beetle outbreak in the 1940s (Veblen et al., 1991). Also similar to Veblen et al. (1991), post-infestation forests in this study were characterized by increases in growth of mountain hemlock present prior to outbreak rather than increases in seedling recruitment. Mountain hemlock seedlings actually declined in cover from 1987 to 2000 in the Kenai Mountains and likely represented a transition of seedlings to saplings with little new seedling recruitment. Understory mountain hemlock can persist in the low light conditions in mature forests and then grow rapidly when canopy trees are removed or die (Seidel, 1985; Means, 1990).

Forests of the southern Kenai Lowland were dominated by continuous stands of mature white spruce prior to the infestation and these forests experienced the most substantial reductions in spruce volume, tree size class, and stand structure (van Hees, 2005). In many of these stands spruce beetles killed most of the overstory white spruce (87% reduction in white spruce basal area), converting forests to herbaceous types and woodlands. Forbs and grasses were the dominant understory plants prior to the beetle infestation, and increased light allowed competitive species, such as bluejoint and fireweed, to increase substantially in some stands. These plant responses were similar to those observed in the Resurrection Creek valley in the Kenai Mountains in which bluejoint and fireweed abundance increased and plant species richness decreased from 1980 to 1991 following both spruce beetle infestation and prescribed fire (Holsten et al., 1995). However, such responses did not characterize infested forests across the Kenai Peninsula in this study. Bluejoint expansion in particular was restricted to the southern Kenai Lowland but was not associated with decreased species richness. In a review of the effects of prescribed burning on plant communities in the Kenai Mountains, the prescribed burn in the Resurrection Creek study (Holsten et al., 1995) was the most extreme example of bluejoint expansion of the 17 burns reviewed (Boucher, 2003). Bluejoint thrives on moist, nutrient-rich sites (Corns and Annas, 1986; Lieffers et al., 1993; Ringius and Sims, 1997) with deep loamy soil such as those of the Resurrection Creek valley (Boucher, 2003). Thus specific site conditions are likely necessary for grasses and forbs to proliferate following spruce beetle outbreaks.

Few changes in vegetation composition were noted among forests on the northern Kenai Lowland and Gulf Coast regions and were likely related to the pre-infestation composition of forests in these regions. On the northern Kenai Lowland, white spruce was often a secondary canopy species to paper birch, black spruce, and aspen in mixed forests; the overall mortality of spruce in this area was low (28% reduction in white spruce basal area) with no uniform directional shift in vegetation composition. On the Gulf Coast, mixed forests of mountain hemlock and Sitka spruce suffered the lowest regional mortality of spruce (22% reduction in Sitka spruce basal area) during the outbreak. Sitka spruce are poor hosts for supporting spruce beetle reproduction (Holsten and Werner, 1990) which likely

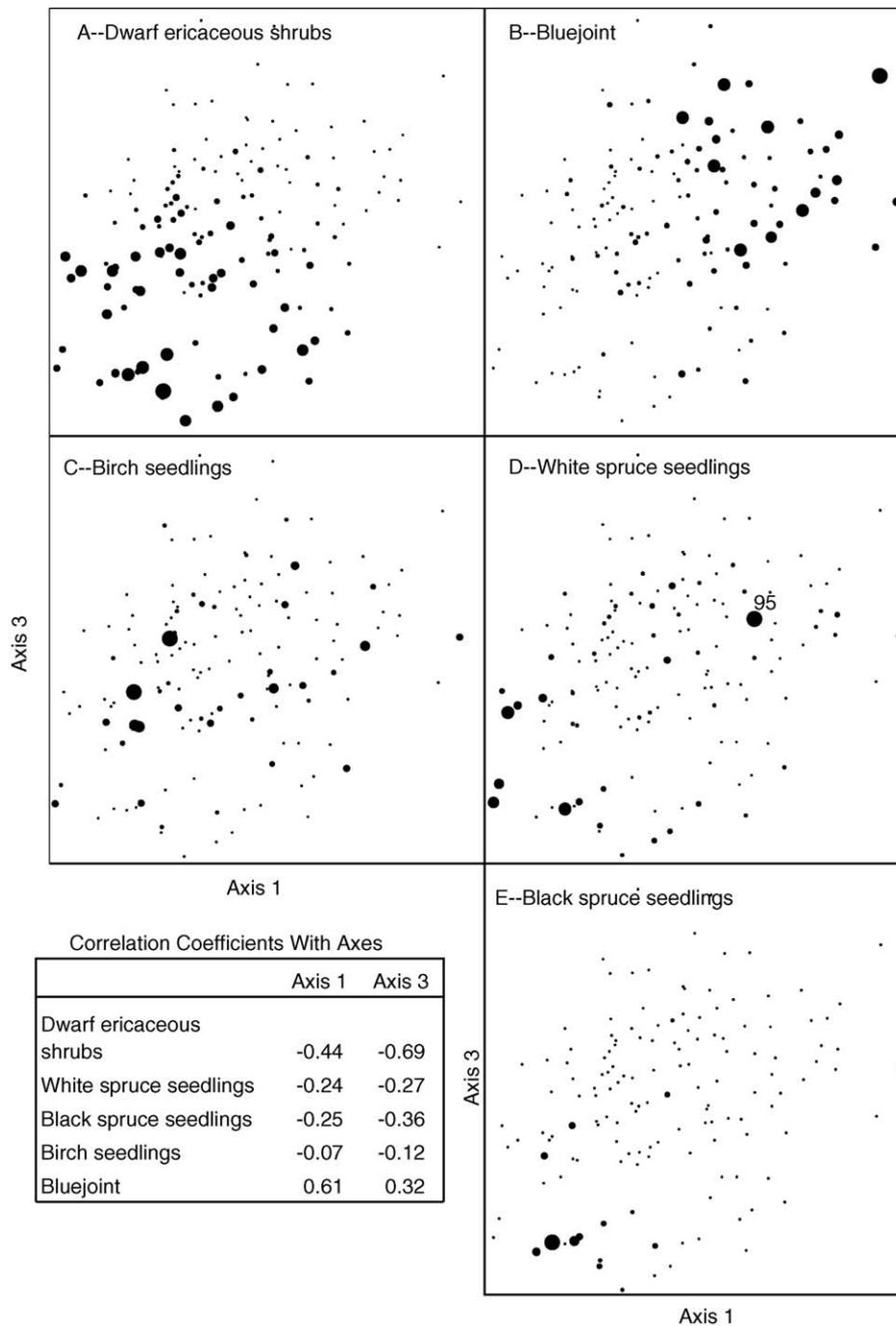


Fig. 5. Relationship of ordination axes with the cover of: (A) dwarf ericaceous shrubs and (B) bluejoint, and seedling densities of: (C) paper birch, (D) white spruce, and (E) black spruce on the Kenai Lowland, Kenai Peninsula, Alaska. Correlation coefficients between ordination axes and plant cover or seedling densities are included. Spruce seedlings generally co-occurred with ericaceous shrubs and were in low densities in areas with high bluejoint cover. Paper birch seedling densities were not correlated with either of the ordination axes. Correlation coefficient of $r > 0.17$ and $r < -0.17$ were at $\alpha < 0.05$ for a sample size of 144 plots (Zar, 1984). Correlations of ordination axes and environmental and vegetation variables are shown in Fig. 5 (inset).

influenced the low levels of spruce mortality during the outbreak and related vegetation change in this region.

Although this study took place in the immediate aftermath of the spruce beetle outbreak, most areas, including those most heavily impacted by spruce beetles, showed signs of forest regeneration (van Hees, 2005). An abundance of bluejoint, a species that can expand rapidly after canopy reduction (Greenway and Lieffers, 1997), has been shown to form a insulating sod

layer that both reduces soil temperature (Hogg and Lieffers, 1991) and inhibits the establishment and growth of spruce and birch seedlings (Cater and Chapin, 2000). However, this study did not find that increases in bluejoint cover resulted in reductions in spruce and birch recruitment. Only 3% of the 115 plots in this study had poor prospects for forest regeneration in the near future owing to abundant bluejoint (>20% cover) and lack of overstory trees (<10% stocked). Furthermore, most of the

plots that showed increases of bluejoint cover of >10% had no seedlings during either time period or showed little change in seedling abundance between measurements.

While the stocking of birch and spruce on many of the plots sampled would be considered poor by forest management standards, surviving tree canopies may have provided shade sufficient to limit bluejoint expansion and thereby increase the likelihood of gradual spruce and birch establishment. Most of the plots that had abundant bluejoint but no tree seedlings were on benches, toe slopes, and valleys flanking the Caribou Hills in the southern Kenai Lowland (U.S. Forest Service, Unpublished data). These sites typically had soils that favor bluejoint expansion (Lieffers et al., 1993; Boucher, 2003) and may be particularly slow to reforest following the spruce beetle outbreak.

5. Conclusions

Spruce beetles have long been an integral part of the disturbance regime of forests on the Kenai Peninsula and will continue to be a major challenge to forest management in the region in the future. In this study, both spruce mortality and related changes in vegetation were quite variable on the Kenai Peninsula suggesting that forest management will not always be uniform in response to large-scale spruce beetle infestations. For example, mixed-forests with spruce were not severely impacted by the recent spruce beetle outbreak and generally exhibited little change in vegetation structure and composition. Therefore mixed forests may not be a priority for pre- or post-infestation forest management on the Kenai Peninsula. In contrast, beetle-induced mortality in the spruce-dominated forests of the southern Kenai Lowland was substantial, changed much of the forested area to woodlands and herbaceous types, and was linked to both bluejoint expansion and general low densities of tree seedlings. These forests could therefore be the focus of management activities aimed towards reforestation, wildlife habitat improvement, hazardous fuel reductions, or prevention of future outbreaks on the Kenai Peninsula.

This study and others suggest that post-disturbance bluejoint expansion occurs on sites with specific characteristics (Lieffers et al., 1993; Holsten et al., 1995; Boucher, 2003). However, long-term studies have shown that bluejoint peaks in abundance soon after overstory tree removal and then declines to pre-disturbance levels over time (Schulz, 2000; Wurtz and Zasada, 2001). Thus it is not clear whether bluejoint is a short- or long-term impediment to forest regeneration that should be actively managed following spruce beetle outbreaks.

Warm temperatures will continue to fuel future infestations of spruce beetles (Berg et al., 2006) by causing widespread drought stress of spruce (Barber et al., 2000) and accelerating the lifecycle of spruce beetles (Werner and Holsten, 1985). The current trend in warming summer temperatures on the Kenai Peninsula appears to have changed the pattern of spruce beetle outbreaks from short-lived episodes curtailed by cool weather to longer and more intense outbreaks (Berg et al., 2006) with broad but variable short-term effects on the composition and structure of forest vegetation as evidenced by this study. In areas with high spruce mortality and grass expansion, future

forests may not look like the forests that preceded them. Future monitoring of the plots in this study would help better understand and therefore manage long-term succession of forests following this and future outbreaks of spruce beetles in the region. Such trajectories in plant succession may be particularly difficult to predict owing to the effects of climate warming and related landscape drying on Kenai Peninsula vegetation (Klein et al., 2005).

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Appendix A

Common and scientific names of plant species included in this paper. Nomenclature follows the U.S. Natural Resources Conservation Service (2005).

Common name	Scientific name
Trees	
Paper birch	<i>Betula papyrifera</i>
White spruce	<i>Picea glauca</i>
Black spruce	<i>Picea mariana</i>
Sitka spruce	<i>Picea sitchensis</i>
Black cottonwood	<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>
Quaking aspen	<i>Populus tremuloides</i>
Mountain hemlock	<i>Tsuga mertensiana</i>
Shrubs	
Sitka alder	<i>Alnus viridis</i> ssp. <i>sinuata</i>
Dwarf birch	<i>Betula nana</i>
Labrador tea	<i>Ledum groenlandicum</i>
Marsh Labrador tea	<i>Ledum palustre</i>
Rusty menziesia	<i>Menziesia ferruginea</i>
Devil's club	<i>Oplopanax horridus</i>
Currant	<i>Ribes</i> sp.
Prickly rose	<i>Rosa acicularis</i>
Red raspberry	<i>Rubus idaeus</i>
Salmonberry	<i>Rubus spectabilis</i>
Willow	<i>Salix</i> sp.
Red elderberry	<i>Sambucus racemosa</i>
Mountain ash	<i>Sorbus sitchensis</i>
Beauverd spiraea	<i>Spiraea stevenii</i>
Tall blueberry	<i>Vaccinium ovalifolium</i>
Forbs and sub-shrubs	
Yarrow	<i>Achillea</i> sp.
Monkshood	<i>Aconitum delphinifolium</i>
Goat's beard	<i>Aruncus dioicus</i>
Fireweed	<i>Chamerion angustifolium</i>
Three-leaved gold thread	<i>Coptis trifolia</i>
Bunchberry	<i>Cornus canadensis</i>

Appendix A. (Continued)

Common name	Scientific name
Crowberry	<i>Empetrum nigrum</i>
Sweet bedstraw	<i>Galium triflorum</i>
Northern commandra	<i>Geocaulon lividum</i>
Northern geranium	<i>Geranium erianthum</i>
Alpine heuchera	<i>Heuchera glabra</i>
Twin flower	<i>Linnaea borealis</i>
Side bells	<i>Orthilia secunda</i>
Lousewort	<i>Pedicularis</i> sp.
Jacob's ladder	<i>Polemonium</i> sp.
Liverleaf wintergreen	<i>Pyrola asarifolia</i>
Nagoon berry	<i>Rubus arcticus</i>
Five-leaf bramble	<i>Rubus pedatus</i>
Sitka burnet	<i>Sanguisorba canadensis</i>
Twisted stalk	<i>Streptopus amplexifolius</i>
Foam flower	<i>Tiarella trifoliata</i>
Star flower	<i>Trientalis europaea</i>
Bog blueberry	<i>Vaccinium uliginosum</i>
False hellebore	<i>Veratrum viride</i>
Grasses	
Bluejoint	<i>Calamagrostis canadensis</i>
Ferns and fern allies	
Lady fern	<i>Athyrium filix-femina</i>
Shield fern	<i>Dryopteris expansa</i>
Common horsetail	<i>Equisetum arvense</i>
Woodland horsetail	<i>Equisetum sylvaticum</i>
Oak fern	<i>Gymnocarpium dryopteris</i>
Stiff clubmoss	<i>Lycopodium annotinum</i>
Beach fern	<i>Phegopteris connectilis</i>

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