Managing forests infested by spruce beetles in south-central Alaska: Effects on nitrogen availability, understory biomass, and spruce regeneration

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Abstract

In Alaska, an outbreak of spruce beetles (*Dendroctonus rufipennis*) recently infested over one million hectares of spruce (*Picea* spp.) forest. As a result, land management agencies have applied different treatments to infested forests to minimize fire hazard and economic loss and facilitate forest regeneration. In this study we investigated the effects of high-intensity burning, whole-tree harvest, whole-tree harvest with nitrogen (N) fertilization, and conventional harvest of beetle-killed stands 4 years after treatment, as well as clear-cut salvage harvest 6 years after treatment. We measured available soil ammonium and nitrate and estimated N loss from leaching using in situ cation and anion resin exchange capsules. We also assessed spruce regeneration and responses of understory plant species. Availability and losses of N did not differ among any of the management treatments. Even a substantial application of N fertilizer had no effect on N availability. Spruce regeneration significantly increased after high-intensity prescribed burning, with the number of seedlings averaging 8.9 m^{-2} in burn plots, as compared to 0.1 m^{-2} in plots that did not receive treatment. Biomass of the pervasive grass bluejoint (*Calamagrostis canadensis*) was significantly reduced by burning, with burn plots having 9.5% of the *C. canadensis* biomass of plots that did not receive treatment. N fertilization doubled *C. canadensis* biomass, suggesting that N fertilization without accompanying measures to control *C. canadensis* is the least viable method for promoting rapid spruce regeneration.
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1. Introduction

During the 1990s, an already pervasive epidemic of spruce beetle intensified among forests of south-central Alaska. Approximately 1.3 millon ha of white (*Picea glauca*), Lutz (*Picea × lutzii*), and Sitka spruce (*Picea sitchensis*) forest were impacted from 1989 to 2000 in Alaska (Werner et al., 2006), reportedly the world's largest spruce beetle outbreak (Packee, 1997). Spruce beetle activity in Alaska subsequently subsided due to a depletion of suitable host spruce (U.S. Forest Service, 2000) but the outbreak left forest managers with the task of managing over 1 million ha of forest with dead trees. A significant increase in surface fuel loading coupled with increases in fuel height has increased the risk of wildfire in forests impacted by the spruce beetle (See, 1998). Downed white spruce fuels alone increased significantly by as much as 7.6 tonnes per ha per size category between 1987 and 2000

(Schulz, 2003). At the same time, a dearth of seed trees coupled with competition with bluejoint (*Calamagrostis canadensis*) presents a challenge to forest regeneration (Eis, 1981). Clear-cut salvage logging has been posed as a means to reduce fire hazard, salvage valuable timber, and reduce further propagation of spruce beetle populations. Prescribed fire has been proposed to reduce fuel loads of beetle-killed forests (Ross et al., 2001). In either case, rapid reforestation is a dominant management goal, as both the timber industry and some wildlife proponents would like to see the boreal forest restored (Packee, 1997).

Forest managers must evaluate ecosystem effects of different management practices to help decide which practices best attain reforestation goals. Such decisions are complicated by the possibility that insect outbreaks may increase nitrogen (N) availability (Lovett and Ruesink, 1995). Insects can cause significant increases in litter fall, and decreases in plant N uptake via mass defoliation and plant mortality. Additionally, beetle frass, a mixture of fecal material and boring dust, and dead beetle remains can substantially increase total N inputs via litterfall (Hollinger, 1986; Lerdau, 1996). For example,

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Hollinger (1986) found that total N flow to the ground more than doubled from stands of California oak (*Quercus agrifolia*) experiencing an outbreak of the California oak moth (*Phryganidia californica*). Salvage logging and burning can decrease the capacity of the ecosystem to retain such N increases because the removal of trees often decreases N immobilization by decreasing the ratio of carbon to nitrogen (C/N) and increasing soil moisture (Vitousek and Melillo, 1979) and soil pH (Hendrickson et al., 1989). Some management practices may thus cause ecosystem N losses (Lindo and Visser, 2003), which could in turn affect succession and spruce regeneration.

In addition to being potentially affected by changes in nutrient availability, spruce forest regeneration can be slowed by competition from herbaceous plants and grasses. In much of Alaska, one of the greatest inhibitors to spruce regeneration after disturbance is the grass *C. canadensis* (Eis, 1981; Powelson and Lieffers, 1992; Wurtz, 2000). Spruce seeds may become suspended in this grass and never reach the forest floor, desiccating before germinating roots can penetrate the soil. Those that become established must compete with the grass for light (Wurtz, 2000). In winter, small seedlings may become flattened by dead grass beneath snow loads (Lieffers et al., 1993). Additionally, the thick rhizome mats of *C. canadensis* decrease soil temperatures to those normally below the threshold of spruce tolerance (Lieffers et al., 1993; Holsten et al., 1995). *C. canadensis* naturally occurs in small patches within actively growing spruce stands. However, when exposed to increased light after logging or tree mortality, *C. canadensis* spreads rapidly via its rhizomes. Within 1–2 years, grass can dominate the vegetation cover (Wurtz, 2000).

This study investigated which management practices minimize N losses and which practices most effectively promote rapid forest regeneration among forests infested by spruce beetles. To address our questions, we made use of five separate management treatments, which were established as part of a larger investigation of successional patterns in spruce beetle infested ecosystems (Patel-Weynand and Gordon, 1999). These treatments were control burning, selective whole-tree harvest of beetle-killed trees, selective whole-tree harvest followed by N fertilization, selective harvest of the tree stems only, and no treatment. We also compared infested forests that were clear-cut to infested forests left untreated in the Copper River Basin, Alaska. Specifically we tested the following hypotheses:

(1) Burning will expose mineral soil and decrease competition to spruce seedlings. Therefore, spruce regeneration will be greater in burn plots.
(2) Burning will increase N leaching from soil, at least in the short term, due to increased mineralization and reduced plant and microbial N uptake.
(3) Harvesting trees will remove carbon from the ecosystem, reducing the C/N ratio in soil. Therefore, depending on the amount of material removed, harvesting will increase leaching losses of N.
(4) Harvesting will increase the amount of available light, and change community dynamics to favor early successional species.

(5) N fertilization will substantially reduce soil C/N, enhancing N leaching.
(6) N fertilization will increase productivity of forbs and grasses.
(7) Alternately, due to severe N limitation of plants and microorganisms (Schulze et al., 1994), any increases in N pools will be immobilized. Therefore, there will not be any long-term management effect on N cycling.

2. Methods

2.1. Study sites

We conducted the majority of this study near Cooper Landing on the Kenai Peninsula, Alaska (Fig. 1), one of the regions of Alaska most heavily impacted by the spruce beetle (Wittwer, 2000). The region annually receives 55 cm of precipitation and 116 cm of snowfall. Daily air temperatures average −8 °C in December and January and +13 °C in July (Weatherbase, 2002). The treatment plots were divided between two sites, which differed in vegetation community and elevation, Juneau Creek at 60°29′N, 149°35′W and an elevation of 335 m and Dave's Creek at 60°31′N, 149°37′W and an elevation of 183 m. At Juneau Creek, the forest was mixed, consisting of Lutz spruce (*Picea* × *lutzii*), mountain hemlock (*Tsuga mertensiana*) and black spruce (*Picea mariana*). The dominant shrub was rusty menziesia (*Menziesia ferruginea*). Dave's Creek was characterized by white spruce and birch (*Betula papyrifera*) in the overstory with a dominant *C. canadensis* understory.

In addition to the plots on the Kenai Peninsula, we also established treatment plots in the Copper River Basin, Alaska between 61°31′N, 144°19′W and 61°24′N, 143°07′W within the administrative boundaries of Wrangell-St. Elias National Park and Preserve (WRST) (Fig. 1). This region is characterized by a very dry and cool climate, with annual precipitation averaging about 45 cm. Average maximum air temperatures range from −18 °C in December and January to +19 °C in July (Wesser and
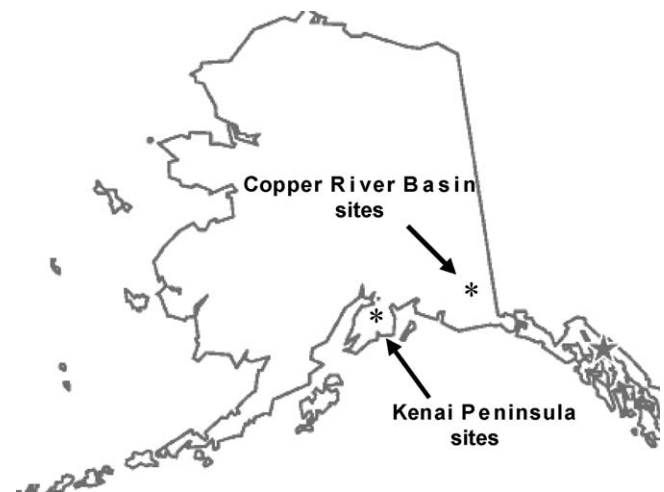

Fig. 1. Study locations in Alaska are denoted with a *.

Allen, 1999). White spruce (*Picea glauca*) and mixed communities of white spruce and balsam poplar (*Populus balsamifera*) or aspen (*Populus tremuloides*) dominated the overstory, while dominant understory shrubs included Labrador tea (*Ledum palustre*) and lingonberry (*Vaccinium vitis-idaea*).

2.2. Treatments

We established three 30 m × 30 m plots in each of five treatments at each of the two sites on the Kenai Peninsula. The treatments were applied in 1997 and included (1) control burning (Burn), (2) selective whole-tree harvest of beetle-killed trees (WTH), (3) selective whole-tree harvest followed by N fertilization (Nitrogen), (4) selective harvest of only the boles (Slash) and (5) no treatment (No Treatment). In all plots with the exception of No Treatment, beetle-killed spruce were cut into bolts and moved 30 m outside of the boundaries of the plots, using a winch to minimize soil disturbance. Burn plots were further divided into four 5 m × 5 m subplots, where de-limbed slash from the beetle-killed spruce and woody material greater than 10 cm in diameter were burned in piles. On WTH plots, slash was also moved to 30 m outside of the plots. Nitrogen plots were treated with a total of 250 kg N ha^{-1} as ammonium nitrate. To minimize N losses in runoff, fertilizer was applied in two separate applications, one in mid-June and the other in late July of 1997. Slash less than 10 cm in diameter was spread uniformly across all Slash plots (Patel-Weynand and Gordon, 1999).

In addition to the plots on the Kenai Peninsula, we studied ten 20 m × 20 m plots in the Copper River Basin: five clear-cut salvage-logged plots and five No Treatment plots. The logged sites were on Ahtna Native Corporation land within the boundaries of WRST, had nearly 100% of spruce infested by spruce beetles, and were logged in 1995. The salvage logging method had been clear-cutting, leaving behind small patches of unmerchantable trees (Maricle, 2001). Slash had been left in place on the forest floor but was not spread uniformly as in the Kenai treatments. We selected No Treatment plots from plots that were established by a National Park Service research team in 1997 and 1998 as part of a broader study examining the impacts of spruce beetle on plant communities (Allen et al., 2006). Percent of trees killed by spruce beetles among the No Treatment plots was between 55 and 95%. Direct comparisons between logged sites on the Kenai and Copper River Basin were not made because the two regions differed in climate and soil. Instead, we compared the degree by which the communities in logged treatments deviated from No Treatment.

2.3. Nitrogen availability

In order to assess potential N cycling changes caused by management of beetle-killed spruce, we assessed ammonium (NH_4^+) and nitrate (NO_3^-) availability and estimates of leaching losses at all sites using buried cation and anion resin exchange capsules (Skogley and Dobermann, 1996). We estimated nitrogen losses through leaching by measuring the

amount of N available below the rooting zone. In each Kenai plot, we deployed four capsules in each treatment plot, 2–8 June 2001 using PVC access tubes. Capsules were made by Unibest Incorporated (Bozeman, MT) and access tubes were made by WECSA Corporation (Fort Collins, CO). We placed two capsules 5 cm below the surface of the mineral soil, and two capsules at depths between 45 and 75 cm, depending on depth of the target soil horizon. In each Copper River Basin plot, we placed two capsules 5 cm below the soil surface, 11 and 12 June 2001. We retrieved capsules 8 weeks later (4 August for Kenai plots and 8 and 9 August for Copper River Basin plots), washed them with de-ionized water, stored them in zip-lock bags, and shipped them to a laboratory. Once at the lab, resin capsules were air dried and extracted with 2 M KCl as follows: we added the capsules to 20 ml of solution, placed them on a shaker table for 60 min, added them to another 30 ml of solution, and then placed the capsules on the shaker table for 60 min. The combined 50 ml of extract were analyzed for NH_4^+ and NO_3^- concentrations (μg N/capsule) using a flow-injection Lachat automated colorimetry system. We used one-way analysis of variance (ANOVA) (SYSTAT for Windows, Version 9, SYSTAT Software Inc., Richmond, CA) to compare both NH_4^+ and NO_3^- availability across treatments for Kenai samples, and a two-sample *t*-test for Copper River Basin samples.

2.4. Understory biomass and spruce regeneration

In July 2001, we measured vegetation cover and harvested biomass of understory plants at Kenai treatments in 1 m × 1 m subplots within each plot. Subplots were evenly distributed along alternating sides of diagonal transects across each plot (except plots in the burn treatment as described below), with six subplots at the Juneau Creek site and five subplots at Dave's Creek. In Burn treatment plots at both sites, we sampled two 1 m × 1 m subplots in each of three 5 m × 5 m Burn subplots. In order to minimize edge effects, we placed the 1 m × 1 m subplots in the middle of the area where the burn had been the hottest, which averaged 2–3 m^2. We assumed the hottest region of the burn was the portion that exhibited the most fuel consumption as determined by the greatest amount of charred soil.

We visually estimated percent cover of individual plants and moss in each subplot and then clipped and collected above-ground plant material (with the exception of moss) to determine biomass. We separated vegetation by species and characteristic (woody, herbaceous or fruit), placed the samples into paper bags, and then oven dried the samples at 70 °C until a constant dry weight was reached. We cooled and then weighed the dry plant material on an electronic balance to 0.1 g. Data on species richness and abundance of dominant species were log transformed to achieve normality and compared across treatments using one-way ANOVA followed by Fisher's least significant difference (LSD) multiple comparison tests. Because Juneau and Dave's Creek vegetation communities were different from each other, we analyzed the two sites separately.

To characterize diversity of understory vegetation, we examined mean rank/abundance relationships for each treatment using the mean proportion of total biomass for each species for each plot. We calculated the slopes of the rank/abundance curve for each plot and then compared mean slopes across treatments with one-way ANOVA followed by LSD multiple comparison tests.

We estimated fruiting success of the dominant shrub *M. ferruginea* as the dry weight of fruit in each plot divided by the dry weight of the entire above-ground biomass of the plant. We also calculated the ratio of herbaceous growth to woody growth.

In the Copper River Basin, we estimated percent cover of all forbs and grasses at all plots in late June 2001. We haphazardly threw a 1 m^2 circular ring in six different directions from the center of the 20 m × 20 m plots and then visually estimated percent cover within each subplot. Species were not divided by height classification; thus it was possible to have greater than 100% cover for individual sub plots. We compared the percent cover of individual species between treatments using a Kruskal–Wallis non-parametric test.

To determine regeneration of spruce, birch, and hemlock, we measured the height (cm) and counted seedlings within each 1 m^2 subplot. We did not collected seedlings as part of the Kenai biomass survey. We compared the total number of spruce m^{-2} across Kenai treatments and across Copper Basin treatments separately using one-way ANOVA. We used simple linear regression to determine whether numbers of spruce seedlings were related to the availability of NH_4^+ and NO_3^-.

3. Results

3.1. Nitrogen availability and losses

There were no differences in N availability ($F \leq 1.43$; d.f. = 4, 40; $P \geq 0.24$) or losses at any of the Kenai treatments (Fig. 2). Additionally, there were no observed differences in N availability (NH_4^+ or NO_3^-) between Logged and No Treatment plots at the Copper Basin ($t \geq -2.47$; d.f. = 4; $P \geq 0.07$). Spruce regeneration and N availability among Kenai

treatments were not related ($r^2 = 0.04$, $F = 2.16$, $P = 0.15$, $n = 29$).

3.2. Spruce regeneration and understory biomass

The hypothesis that burning would increase spruce regeneration was strongly supported by our data. Burn plots exhibited a greater number of spruce seedlings than all of the other treatments ($F = 11.39$; d.f. = 4, 25; $P < 0.001$), with a mean of 8.9 seedlings m^{-2} in Burn plots, and means of 0.62, 0.28, 0.33, and 0.12 seedlings m^{-2} in WTH, Nitrogen, Slash and No treatment plots, respectively. This difference was observed only for spruce seedlings <5 cm in height; there was no difference in abundance of spruce seedlings >5 cm. Spruce seedling densities did not differ among the WTH, Nitrogen, Slash and No Treatment treatments (Fig. 3a). The same pattern of increased seedling abundance on Burned plots was observed for birch ($F = 6.40$; d.f. = 4, 25; $P = 0.001$) but not hemlock ($F = 0.51$; d.f. = 4, 25; $P = 0.73$) (Fig. 3b).

Thirty forb and shrub species were observed across Kenai plots combined and 30 forb and shrub species were documented among Copper River Basin plots. Average number of species per plot did not differ across Kenai treatments ($F = 2.03$; d.f. = 4, 25; $P = 0.12$) or Copper River Basin treatments
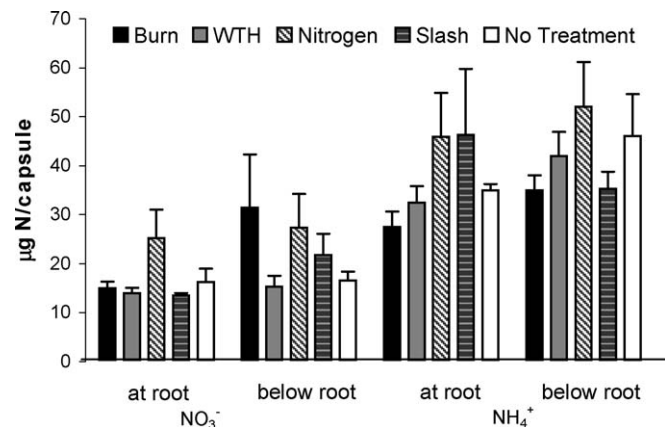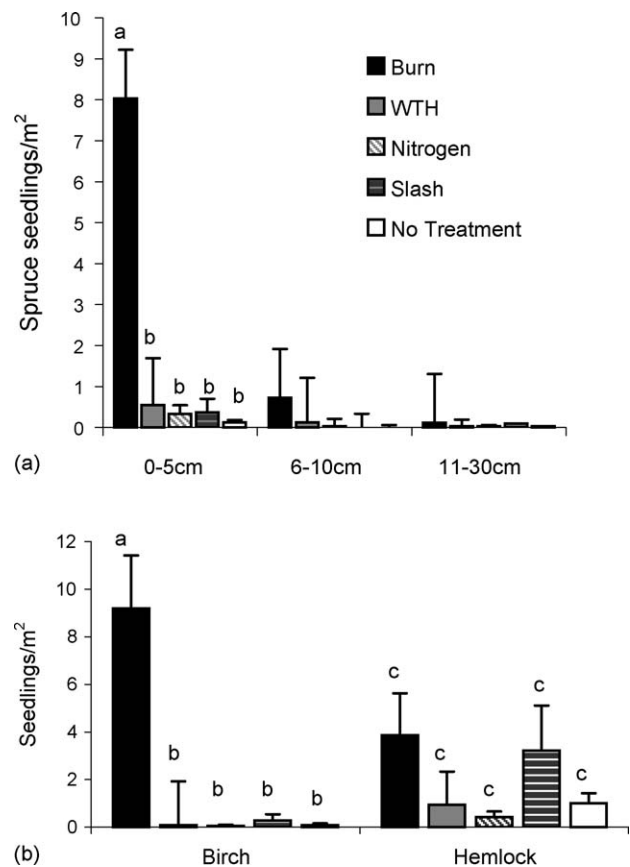

Fig. 2. N availability and leaching at Kenai Peninsula, Alaska plots as indicated by N availability below rooting zone. Values shown are treatment mean ± standard error bars ($n = 6$). Significant differences were not detected at the 0.05 alpha level.

Fig. 3. Numbers of (a) spruce and (b) birch and hemlock seedlings <10 cm in height at Kenai Peninsula, Alaska plots. Values shown are treatment mean ± standard error bars ($n = 6$). Means with different letters are significantly different from each other at a 0.05 alpha level.
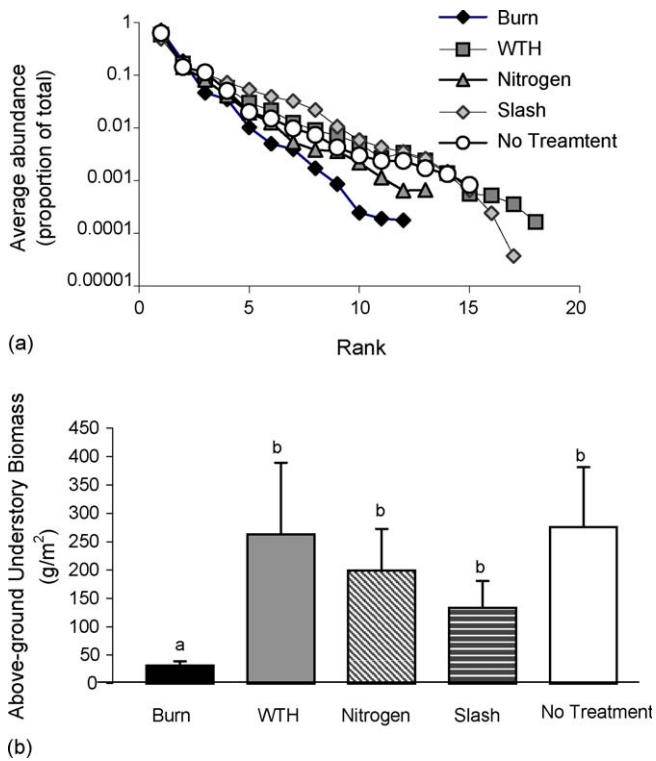
Fig. 4. Above-ground understory biomass at Kenai Peninsula, Alaska plots characterized by (a) rank abundance curves generated by averaging across all replicates in a treatment and (b) treatment mean values of above-ground understory biomass ± standard error bars ($n = 6$). Means with different letters are significantly different from each other at a 0.05 alpha level. Slopes of rank abundance curves were significantly different ($F = 3.37$, $P = 0.025$) between Slash and Nitrogen ($P = 0.016$) and between Slash and Burn treatments ($P = 0.002$).
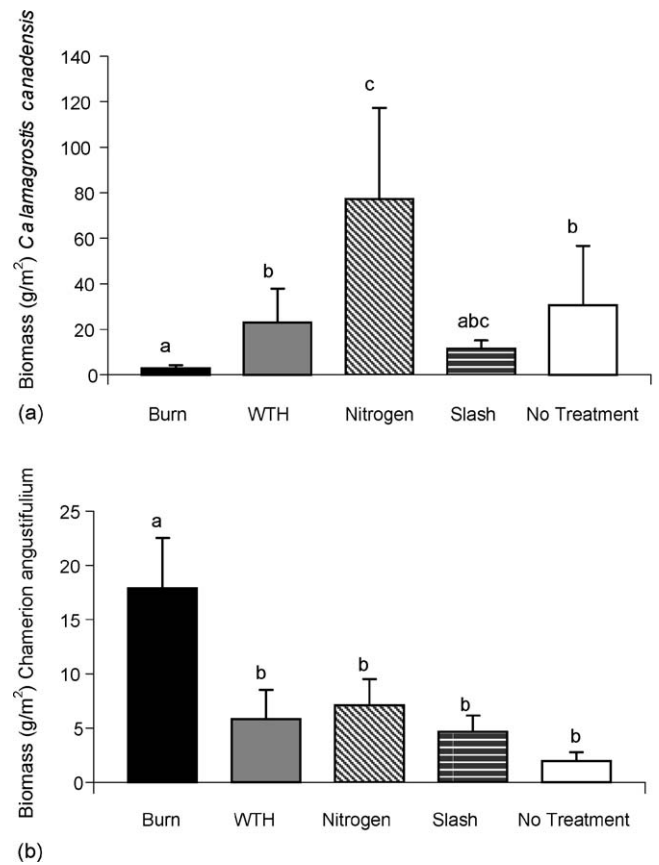

Fig. 5. Above-ground biomass of (a) *Calamagrostis canadensis* at Dave's Creek plots ($n = 3$) and (b) *Chamerion angustifolium* at all Kenai Peninsula, Alaska plots ($n = 6$). Values shown are treatment mean ± standard error bars. Means with different letters are significantly different from each other at a 0.05 alpha level.

($T = 0.50$; d.f. = 4; $P = 0.64$). However, Kenai treatments differed in evenness ($F = 3.36$; d.f. = 4, 25; $P = 0.03$) (Fig. 4a). Burn plots were most heavily dominated by one species, fireweed (*Chamerion angustifolium*), with relatively few rare species and Slash plots exhibited higher evenness. Slopes from rank abundance curves differed between Burn and Slash (LSD, $P = 0.002$) and Slash and Nitrogen (LSD, $P = 0.016$) treatments. Overall, total understory biomass was relatively low in Burn plots ($F = 3.63$, $P = 0.018$) (Fig. 4b).

Biomass of *C. canadensis* varied across Dave's Creek treatments ($F = 8.33$; d.f. = 4, 63; $P < 0.001$), with average biomass less on Burn plots than all other treatments except Slash and greatest among Nitrogen plots. Burn plots had 9.5% of the *C. canadensis* biomass measured in No Treatment plots. Nitrogen plots had 2.5 times more biomass of *C. canadensis* than No Treatment plots and significantly more than Burn, No Treatment and WTH plots (Fig. 5a).

Average biomass of *C. angustifolium* was greatest in the Burn treatment and least in the No Treatment ($F = 3.72$; d.f. = 4, 25; $P = 0.016$). With 9.6 times greater *C. angustifolium* biomass than in No Treatment plots, Burn plots exhibited greater *C. angustifolium* biomass than all other treatments (LSD, $P = 0.001$ for No Treatment, $P = 0.078$ for N, $P = 0.021$ for Slash and $P = 0.018$ for WTH) (Fig. 5b).

The dominant shrub at Juneau Creek, *M. ferruginea* exhibited differences across treatments. The plant was absent among Burn plots and its fruiting success was relatively low in the Slash treatment ($F = 20.21$; d.f. = 4, 10; $P < 0.001$; LSD, $P < 0.001$ for No Treatment and WTH, $P = 0.043$ for N) (Fig. 6). The ratio of herbaceous growth to woody growth was also greatest in Slash plots and its biomass the least next to the Burn treatment.

Another important difference in vegetation was the reduction in moss cover in the Nitrogen treatment ($F = 3.52$; d.f. = 4, 136; $P = 0.009$). In Nitrogen plots, moss cover averaged less than half as much as in No Treatment plots and was lower than that of all other treatments (LSD, $P = 0.001$ for No Treatment, 0.009 for Burn, 0.029 for WTH, 0.004 for Slash) (Fig. 7).

While the Kenai WTH treatment resembled No Treatment as far as most of the parameters studied, Copper River Basin logged plots differed more substantially from No Treatment in understory species composition. The clear-cut plots exhibited a high abundance of early successional species including *Rubus idaeus* (Kruskal–Wallis = 7.52, $P = 0.023$), *Rosa acicularis* (Kruskal–Wallis = 4.73, $P = 0.094$), and *Equisetum* spp. (Kruskal–Wallis = 10.63, $P = 0.005$). These species were either absent or sparse in Copper River Basin No Treatment plots (Fig. 8).
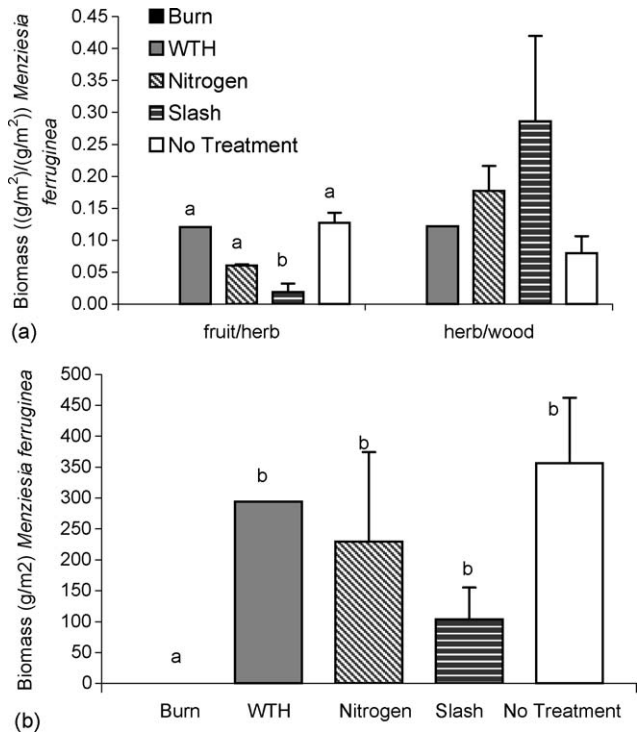
Fig. 6. (a) Fruiting success (measured by ratio of fruit mass to mass of herbaceous growth) and ratio of herbaceous to woody growth of *Menziesia ferruginea* at Juneau Creek. (b) Total above-ground biomass of *M. ferruginea*. Values shown are treatment mean ± standard error bars ($n = 3$). Means with different letters are significantly different from each other at a 0.05 alpha level.
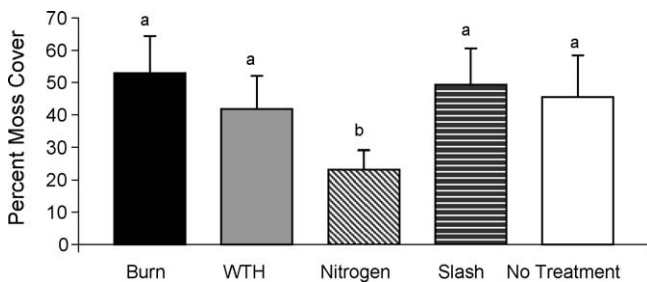

Fig. 7. Percent moss cover at Kenai Peninsula, Alaska plots. Values shown are treatment mean ± standard error bars ($n = 6$). Means with different letters are significantly different from each other at a 0.05 alpha level.
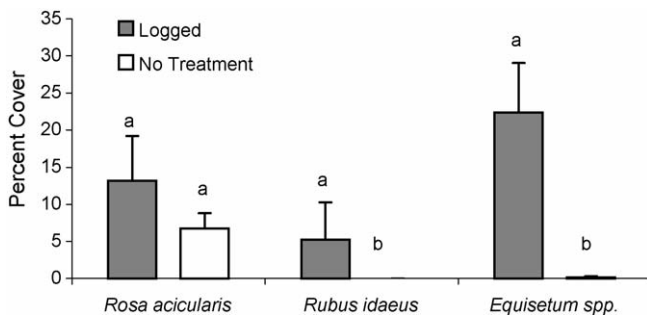

Fig. 8. Percent cover of *Rosa acicularis*, *Rubus idaeus* and *Equisetum* spp. on Copper River Basin, Alaska plots. Values shown are treatment mean ± standard error bars ($n = 5$). Means with different letters are significantly different from each other within individual species at a 0.05 alpha level.

4. Discussion

We did not find evidence to suggest that logging, burning, or even adding 250 kg ha^{-1} N fertilizer to forests infested by spruce beetles influenced soil N availability or leaching losses 4 years after treatment. Even large-scale clear-cut logging appeared to have no effects on N availability 6 years after treatment. These results support the hypothesis that because boreal forests are N limited, potential N inputs are immobilized and N losses are minimal. However, we conducted our study 4 and 6 years after treatment and it is possible that short-term effects on N availability and leaching occurred but were not detected by our investigation. Indeed, the overall effects of N fertilization on N availability in forests are known to be short-lived, lasting less than 3 years (Keeney, 1980). Potential N increases from the beetle outbreak could in fact have been immobilized before the trees were removed. Nitrate immobilization occurred as rapidly as within 15 min of N application in a plantation pine forest in Massachusetts (Bernston and Aber, 2000).

4.1. Treatment effects

Our results suggest that prescribed burning has a large influence on both understory plant communities and spruce seedling regeneration on the Kenai Peninsula. In fact, prescribed fire produced a spruce seedling density that likely exceeds the reforestation goals of most foresters. Our observation that spruce seedling densities were high for seedlings shorter than 5 cm but not for taller seedlings supported the hypothesis that the enhanced recruitment was due to burning and not to some other intrinsic factor such as greater pre-treatment densities of spruce seedlings. Burning also enhanced seedling recruitment for birch but not for hemlock. Birch has been considered a competitor with spruce for light; however, recent research has shown that birch may actually benefit spruce regeneration in the long term. For example, their high root carbon allocation, high tissue nutrient content, and associations with ectomycorrhizal communities may increase nutrient availability to conifers (Simard and Hannam, 2000). At the time of this study, birch and spruce seedlings were the same size, therefore it is not clear whether competition from birch will eventually inhibit or facilitate spruce seedling growth and survival. Future monitoring of our study plots would be useful to determine whether birch enhance or hinder spruce reforestation.

C. canadensis biomass was very low in the Burn treatment, less than 3.0 g m^{-2}. In fact, *C. canadensis* was likely only found growing inside the hottest portion of our small burns due to the spread of rhizomes from survivors in less intensely burned areas within our plots. Further research that takes advantage of larger burn plots is needed to adequately study colonization of *C. canadensis* through time. Other research has found that low temperature burns facilitate *C. canadensis* expansion, while high intensity burns suppress it, presumably by destroying underground rhizomes (Dyrness and Norum, 1983).

The burns in our study had indeed been very hot, baring the mineral soil completely. While the initial bare soil substrate could have been the attribute that permitted germination of the high densities of spruce seedlings we observed, the absence of grass was likely important in the continued growth and survival of the seedlings 4 years after treatment. Lieffers et al. (1993) reported that the height of juvenile white spruce was lower and mortality higher when grown with *C. canadensis* as opposed to shrubs or other trees. *C. canadensis* was also found to delay spring soil warming above 0 °C by 1 month, delaying the onset of spring growth. Intense burn treatments may thus give spruce regeneration two advantages: bare soil substrate for germination and reduced competition from grass for continued growth.

Burning also favored growth of *C. angustifolium*. Like *C. canadensis*, *C. angustifolium* spreads rapidly through rhizomes, quickly taking advantage of increased light in disturbed areas (Landhausser and Lieffers, 1994). Unlike *C. canadensis*, *C. angustifolium* does not suppress spruce seedling success by lowering soil temperatures nor does it cover seedlings in winter and deprive them of light and air (Landhauser et al., 1996). *C. angustifolium* may actually out-compete *C. canadensis* for light especially if it becomes established first (Landhauser et al., 1996). Dyrness and Norum (1983) reported that *C. angustifolium* became established 2 years before *C. canadensis* in heavy burns. This facilitation of *C. angustifolium* colonization may be a third advantage to spruce regeneration offered by hot fires.

Unlike prescribed fire, nitrogen fertilization appears to increase *C. canadensis* biomass and may thus be detrimental to spruce regeneration. Nitrogen fertilization may have further hindered spruce seedling recruitment by reducing moss cover, the most preferred substrate for spruce regeneration after bare soil (Simard et al., 1998). Nitrogen fertilization therefore may have little beneficial effect upon spruce regeneration unless the grass is removed.

Fruiting success of the dominant shrub *M. ferruginea* was suppressed in the Slash treatment on the Kenai Peninsula. Furthermore, this treatment exhibited the lowest *M. ferruginea* biomass next to the Burn treatment, and the greatest ratio of woody growth to herbaceous growth. These results suggest that growth and productivity of this species was reduced, presumably due to smothering or shading by logging stash. Slash may thus reduce the potential for one or two species to dominate the community. A rank abundance curve (Fig. 4a) showing the Slash treatment to exhibit the greatest evenness supports this hypothesis.

The Kenai selective whole tree harvest treatment resembled the No Treatment in understory plant communities. Neither species diversity, spruce regeneration, nor understory biomass appeared to be altered. Considerable shade was still offered by the trees that were left standing and light available to understory plants was likely insufficient to cause a dramatic change in understory biomass or composition. However, vegetation among clear-cut sites in the Copper River Basin showed more substantial changes in understory species composition. The early successional species *R. acicularis*, *R. idaeus*, and *Equisetum* spp. were abundant on sites that were clear-cut

but did not occur or were scarce among No Treatment sites. These plants are indicative of post-disturbance succession in boreal forests (Timoney et al., 1997; Helm and Collins, 1997) and their abundance suggests this treatment may experience a slower return to spruce forests. Timoney et al. (1997) found that *Equisetum* spp., *R. acicularis* and *R. idaeus* are typical vegetation communities in post-clear-cut boreal forests that bypass the natural early successional communities of alder and willow and subsequently progress rapidly to poplar and birch forests, exhibiting no indications that eventual succession to the original spruce forest will follow. Future monitoring of harvested stands in this study would be useful to test whether spruce or deciduous forests regenerate following clear-cutting in the Copper River Basin.

4.2. Management implications and future research

Where rapid regeneration of spruce forests is the predominant management goal, high-intensity prescribed burning appears to be the best management approach for recruiting spruce seedlings. Selective whole-tree harvest with limited ground disturbance does not appear to influence nitrogen cycling or understory biomass. While it may be an effective method to reduce fuel loads, selective-tree harvest did not facilitate spruce seedling recruitment either. Larger scale salvage logging may facilitate colonization of early successional species that could compete with regenerating spruce seedlings. Nitrogen fertilization is not a recommended management approach, as it enhances productivity of *C. canadensis*. Regardless of treatment, abundant spruce regeneration will rely on an ample supply of seed trees. Spruce are not known to disperse seeds farther than 200 m on average (Timoney and Peterson, 1996). Therefore, a scarcity of seed trees is likely to be a limiting factor to spruce regeneration, especially in the Copper Basin clear-cut sites.

Warmer than average temperatures may have been an important factor fueling the massive 1990s outbreak of spruce beetles (Ross et al., 2001; Berg et al., 2006), suggesting that if temperatures rise as predicted by global climate change models (IPCC, 2001), large-scale outbreaks could continue to plague Alaska. Continued monitoring of managed beetle-killed forests is needed to determine which forest practices promote long-term ecosystem sustainability, while meeting management goals. Analyses of larger scale control burns and birch and spruce growth in these treatments will further illuminate the risks and benefits of undertaking this expensive and difficult management option.

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