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Effects of aspen (*Populus tremuloides*) sucker removal on postfire conifer regeneration in central Alaska

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Abstract: This experiment tests the effects of early canopy development by asexually regenerating aspen (*Populus tremuloides* Michx.) on conifer recruitment after fire in central Alaska. The establishment and growth of three conifer species were observed in response to aboveground removal of aspen suckers for three seasons after burning by wildfire. Of the three species, *Pinus contorta* Dougl. ex Loud. had the most widespread seed germination and showed the strongest negative response to the presence of the aspen canopy. *Picea mariana* (Mill.) BSP and *Picea glauca* (Moench) Voss had low germination and weak or neutral responses to aspen removal. Seedlings of all species accumulated more biomass in the removal treatment. Results from the experiment suggest that competition by aspen early after disturbance can significantly reduce conifer recruitment and growth, an effect that may reinforce the long-term dominance of aspen in asexually regenerating stands.

Résumé : Cette expérience avait pour but de tester les effets sur le recrutement des conifères du développement initial du couvert de peuplier faux-tremble (*Populus tremuloides* Michx.) qui se régénère végétativement après un feu dans le centre de l'Alaska. L'établissement et la croissance de trois espèces de conifères ont été observés en réponse à l'élimination de la partie aérienne des drageons de peuplier faux-tremble pendant trois saisons après le passage d'un feu de forêt. Des trois espèces, *Pinus contorta* Dougl. ex Loud. avait le taux de germination le plus élevé et la plus forte réaction négative à la présence du couvert de peuplier faux-tremble. *Picea mariana* (Mill.) BSP et *Picea glauca* (Moench) Voss avaient un faible taux de germination et une réaction faible ou neutre à l'élimination du peuplier faux-tremble. Les semis de toutes les espèces ont accumulé plus de biomasse dans les traitements où le couvert avait été éliminé. Les résultats de cette expérience indiquent que la compétition du peuplier faux-tremble tôt après une perturbation peut significativement réduire le recrutement des conifères en plus de leur croissance, un effet qui peut à long terme renforcer la dominance du peuplier faux-tremble dans les peuplements qui se régénèrent de façon végétative.

[Traduit par la Rédaction]

Introduction

Negative effects of herbaceous or deciduous plant competition on conifer seedling growth have been well documented in the boreal forest (e.g., Farmer et al. 1988; Morris and MacDonald 1991; Jobidon 1994; Bell et al. 2000; Hangs et al. 2002; MacDonald and Thompson 2003). However, few of these studies have taken place in forests regenerating after natural disturbance or evaluated effects on seedling recruitment in addition to growth (however, see Cater and Chapin 2000). Consequently, there remains little information about how competitive interactions may influence patterns of species establishment and the importance of such interactions in structuring natural forest communities.

Trembling aspen (*Populus tremuloides* Michx.) frequently regenerates after disturbance by suckering, or resprouting from belowground roots, and can rapidly develop a closed canopy (Zasada et al. 1992; Lieffers et al. 2002). In boreal forests, successful recruitment of conifer seedlings is often restricted to the first few years after disturbance (Yarrington and Yarrington 1975; Gutsell and Johnson 2002; Johnstone et al. 2004). As a result, competitive interactions between aspen suckers and conifer seedlings that occur early in stand development may be important to long-term patterns of stand

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composition. The present study tests the potential for early aspen competition to inhibit conifer establishment and growth in asexually regenerating aspen stands, thereby favoring long-term deciduous dominance.

Methods

This study took place in a burned stand of mature trembling aspen located on a flat, glacial outwash plain north of the Alaska Range near the town of Delta Junction, Alaska (63°55′N, 145°44′W). Soils in the area are coarse and well drained, consisting of a thin organic layer (3 cm) and a shallow layer of loess-deposited silt (0–15 cm) on top of alluvial cobbles and gravels. A large wildfire burned the study area in June 1999. The selected prefire aspen stand included a few black spruce (*Picea mariana* (Mill.) BSP) and white spruce (*Picea glauca* (Moench) Voss) stems and had soils similar in texture to those in an adjacent, spruce-dominated forest. These factors suggest the potential for the stand to regenerate to a range of deciduous- or conifer-dominated successional trajectories after fire.

An experiment to test the effects of the aspen sucker canopy on conifer recruitment in the stand was initiated in June 2000, 1 year after the fire. A total of 36 circular, 2 m diameter plots were randomly assigned to either a removal or a control treatment (n = 18 plots/treatment). The aspen-removal treatment consisted of aboveground clipping of all aspen stems, contrasted with a control treatment in which the aspen stems were left intact. Aspen stems were clipped annually to maintain the removal treatment. Biomass of the clipped stems was measured in June 2000 and late August 2002, when the experiment was terminated.

Each experimental plot was divided into six subplots consisting of equilateral triangles (area = 0.28 m^2) arranged in a hexagon. Three of the subplots were randomly assigned to a conifer seeding treatment of black spruce (BS), white spruce (WS), and lodgepole pine (LP; *Pinus contorta* Dougl. ex Loud. subsp. *latifolia* (Engelm.) Critchfield), as these species represent the dominant conifers of the boreal forest in Alaska and adjacent Yukon Territory. Conifer seeds were sown in late June and early September 2000. Each seed application consisted of approximately 0.2 g (0.17, 0.23, and 0.24 g for BS, WS, and LP, respectively) of viable seed scattered on the ground surface within the appropriate subplot. Because seed size varied among the three species, this application rate translated into 472, 317, and 283 viable seeds/m^2 for BS, WS, and LP, respectively. The remaining three subplots were untreated and provided data on natural seedling establishment. Observations during the experiment indicated that naturally recruited seedlings contributed 10% (0.2/2.0 seedlings/m^2) of the spruce seedlings observed in the treated plots. Organic layer depth in the plots averaged 3.0 ± 0.4 (SE) cm of well-decomposed, humic soil (n = 36, based on averages of 8 subsamples per plot).

To separate treatment effects on growth versus establishment, young seedlings of the three conifer species were transplanted into their respective subplots (3 seedlings/subplot) in June 2001. The seedlings were first grown for 4 months in standard, 4 cm diameter forestry containers in a greenhouse at the University of Alaska Fairbanks. At the time of planting in June 2001, they were the size of healthy, 2- or 3-year-old natural seedlings (aboveground biomass averaging 0.7, 0.8, and 1.0 g dry mass for BS, WS, and LP, respectively).

Table 1. Summary of seed germination and net seedling establishment across aspen treatments.

	No. plots with germinating seedlings		No. seedlings per gram viable seed[a]	
	Control	Removal	Control	Removal
Seed germination				
Lodgepole pine	12	16	5.3±1.4	11.9±2.7
Black spruce	1	6	0.2±0.2	1.4±0.6
White spruce	6	7	1.1±0.4	1.8±0.7
Net establishment				
Lodgepole pine	11	16	4.5±1.3	10.5±2.8
Black spruce	1	4	0.2±0.2	0.9±0.4
White spruce	5	3	0.6±0.2	0.5±0.3

[a] Values represent the mean ±1 SE (n = 18).

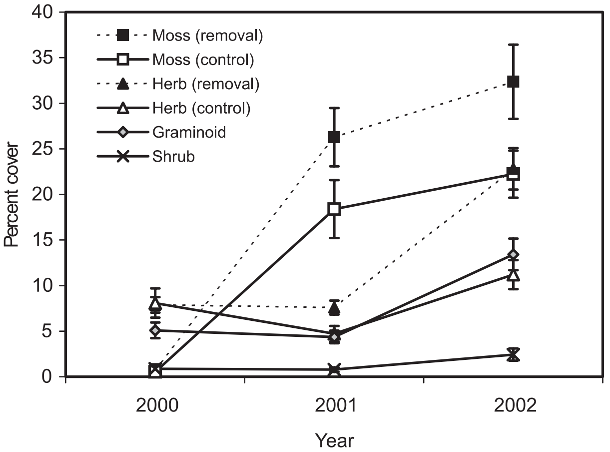
Vegetation cover and the germination and survival of sown seeds or seedlings were monitored during three summers. At peak season (late July) in each year, visual estimates of species cover were made in a 1 m^2 quadrat positioned in the center of each plot. Cover values for individual species were pooled into growth form classes of herbs (nonwoody dicots), graminoids, woody shrubs, and mosses. Plots were surveyed for established seedlings at the beginning, middle, and end of each summer and marked with paperclips. All seeded and transplanted seedlings were harvested on 26 August 2002. Current-year biomass of transplants and total aboveground biomass of sown seedlings were dried in a 60 °C oven for 48 h and then weighed.

Significant differences in variable means between treatments were tested using analysis of variance (ANOVA), with a split-plot design for the species treatment (Cochran and Cox 1992). Treatment effects on cover of vegetation growth forms were tested using repeated-measures, multivariate analysis of variance (MANOVA) followed by univariate ANOVAs on individual growth forms. Analyses of seed germination rates and sown seedling masses were performed separately for each species. Given the high frequency of zero seedling counts (Table 1), randomization tests were used to test for differences in germination and net establishment rates of pine and spruce (Good 2000). Treatment differences in biomass of sown seedlings of pine and pooled black spruce and white spruce were tested using an unbalanced, one-way ANOVA, where plots without germinants were excluded from the analysis. Biomass data were log-transformed and cover data were square-root transformed for analysis. All statistical analyses were performed using SAS version 8.02 (SAS Institute Inc., Cary, N.C.).

Results and discussion

In June 2000, aspen stem densities averaged 18.2 ± 2.3 (mean ± SE) stems/m^2 and decreased during the experiment to 6.1 ± 0.7 stems/m^2. A high density of aspen resprouts followed by rapid thinning is characteristic of aspen stands within the first years after disturbance (Pollard 1971; Zasada et al. 1992; Lavertu et al. 1994; Greene and Johnson 1999; Wang 2003). Although aspen densities declined during the 3 years of study, aspen cover increased from 36% ± 4% to

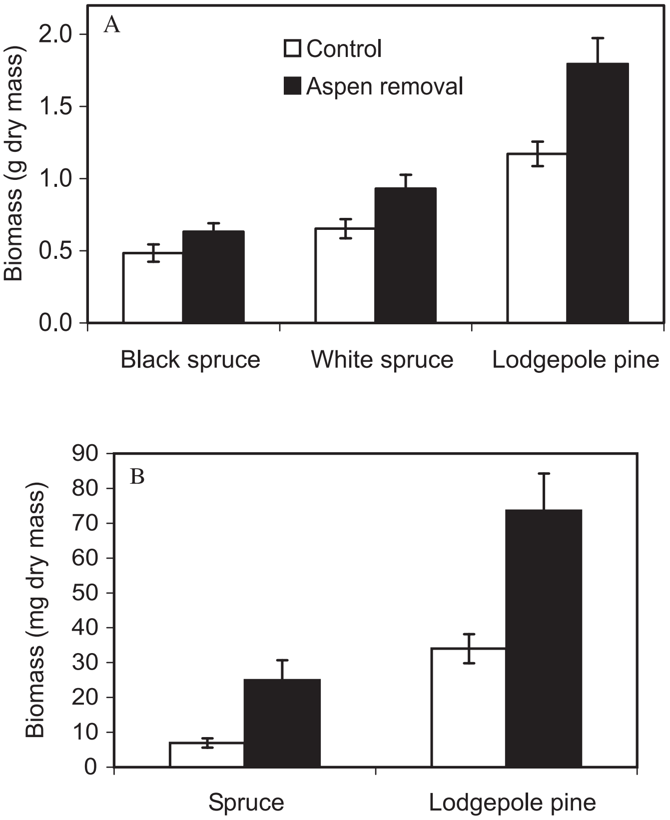
Fig. 1. Vegetation cover in experimental plots for the first 3 years after fire. Species cover was summed into growth form classes: mosses, herbs, graminoids, and shrubs. Values (mean ± 1 SE) are shown separately for aspen control (closed symbols) and removal (open symbols) plots for mosses and herbs. Cover of graminoids and shrubs showed no significant response to the aspen treatment and are represented by means across all plots.



46% ± 3% and biomass increased by a factor of 6 (from 23.3 ± 4.1 to 137.7 ± 15.1 g/m^2). The aspen-clipping treatment successfully reduced the aboveground aspen biomass in the treated plots to very low levels (averaging 0.7 ± 0.1 g/m^2 in the 2002 harvest). Aboveground biomass of aspen was never completely eliminated because of continued resprouting from belowground roots. Sprouting vigor was highest in 2000, when a mean of 17.5 ± 3.5 stems/m^2 were clipped in late July, compared with 2002, when 1.5 ± 0.3 stems/m^2 were clipped in treated plots in late August.

Lodgepole pine showed the highest germination rates of the three conifers included in the experiment and was also the only species to show a strong response to aspen removal (Table 1). Pine germination and establishment rates were significantly higher in aspen removal plots than in controls (t = 2.16 and 1.94, p = 0.02 and 0.05, respectively), leading to an approximate doubling of pine recruitment with aspen removal (Table 1). In contrast, both black spruce and white spruce showed low rates of germination. Although there were trends towards increased germination in aspen removal plots, these effects were weak (BS: t = 1.80, p = 0.06) or nonsignificant (WS: t = 0.87, p > 0.4). Likewise, there were no significant effects of aspen removal on net establishment of either species (t = 1.37 and –0.33, p > 0.1). The low rates of conifer germination observed are unlikely to reflect vegetation competition for suitable seedbeds, as most of the development of ground vegetation (mosses and herbs) occurred after the seed applications in 2000 (Fig. 1). However, identical seeding treatments applied to more optimal seedbeds (100% exposed mineral soil; Jarvis 1966; Greene et al. 1999) in a nearby spruce stand showed similarly low rates of conifer seed germination (means 7.4, 1.4, and 7.5 seedlings/g viable seed for BS, WS, and LP, respectively; n = 6; Johnstone 2003). It is likely that moisture limitation, caused by well-drained soils and frequent wind, was a controlling factor that limited conifer germination. Differences in germination among species reflect differences in seed reserves and initial seedling growth rates (Greene et al. 1999). In this case, the poor germination of black spruce and white spruce reduced the power of the experiment to detect aspen effects on recruitment.

Fig. 2. Aboveground biomass production of (*a*) transplanted and (*b*) sown seedlings (mean ± 1 SE) in aspen removal and control treatments, measured at the end of the 2002 growing season. Biomass values for transplants (*a*) are current-year production (g dry mass) for 2002 (n = 18). Data for sown seedlings (*b*) is total aboveground biomass averaged across plots (n = 11 and 16 for pine and n = 9 and 10 for pooled black spruce and white spruce in control and removal plots, respectively).



Growth of all transplanted conifers responded positively to the aspen removal treatment (ANOVA clip effect, F = 7.56, p = 0.01; clip × species effect, F = 0.31, p = 0.7). Aboveground biomass production in 2002 was an average of 30% lower in control plots than in removal plots (Fig. 2*a*). Growth of sown seedlings showed an even stronger response, with pine and spruce accumulating less than half the aboveground biomass in control plots than in removal plots (F = 8.77 and 8.87, p = 0.007 and 0.008 for pine and spruce, respectively; Fig. 2*b*).

The patterns of seedling growth in response to aspen canopy removal are similar to those in other studies that demonstrate a decline in the growth of conifer seedlings with shading from overstory vegetation (Jobidon 1994; Ter-Mikaelian et al. 1999; MacDonald and Thompson 2003). Effects on seedling establishment may have occurred because of shading and associated microenvironmental effects (Eis 1981; Cater and Chapin 2000) and the effects of increased litter production, which probably reduced the availability of suitable substrates for germination (Purdy et al. 2002). In interpreting seedling responses, it is also important to note that cover of other vegetation types also changed in response to aspen removal (MANOVA for overall clipping × year effect, $F = 4.12$, $p < 0.001$; Fig. 2). Cover of herbs and mosses increased during the experiment by 10–15% in aspen-removal plots compared with controls (herb clipping × year effect, $F = 13.51$, $p < 0.001$; moss clipping effect, $F = 5.14$, $p = 0.03$), while graminoids and shrubs showed no response ($p > 0.1$). Because herbaceous plants can also compete with young tree seedlings (Eis 1981; Bell et al. 2000; Cater and Chapin 2000), the positive response of mosses and herbaceous plants to aspen removal may have partially offset the effects of aspen removal on tree seedlings. Nonetheless, the increased growth and establishment observed in the removal plots demonstrates that the aspen canopy had a stronger effect on conifer seedlings than had the compensatory growth of herbaceous plants.

This study presents some of the first data available on aspen canopy effects on conifer growth in a natural postfire community and is one of the few studies to consider effects on recruitment from seed. The strong pine recruitment response observed here indicates that aboveground competition with aspen resprouts may substantially reduce the potential for conifer recruitment, even immediately after a fire. Because of the importance of early postfire recruitment to mature stand composition (Johnson et al. 1994; Gutsell and Johnson 2002), the effects of early aspen competition can translate into long-term impacts on stand composition. In addition, observed growth responses suggest that where conifer seedlings do become established, slow growth rates will lengthen the period that conifer seedlings remain in the subcanopy. Ultimately, stands that experience both reduced conifer establishment and slow growth are likely to have a lower availability of conifer seed when they burn again, thus favoring the continued dominance of aspen across future disturbance cycles.

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