DIFFERENTIAL EFFECTS OF COMPETITION OR MICROENVIRONMENT ON BOREAL TREE SEEDLING ESTABLISHMENT AFTER FIRE

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Abstract. We used a combination of surveys of natural vegetation and seed-sowing and seedling transplant experiments to determine the relative importance of competition and microenvironmental modification as mechanisms by which understory vegetation influences the establishment of tree seedlings in an Alaskan postfire boreal forest. Seedlings of white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) became established more frequently than expected in patches that were dominated by horsetail (*Equisetum arvense*), and less frequently than expected in patches of bluestem (*Calamagrostis canadensis*) and other vegetation. Similarly, birch and spruce, whether sown directly or transplanted as seedlings into horsetail-dominated patches generally showed greater survivorship, growth, and nitrogen accumulation (for birch only) than did those transplanted into bluestem or quaking aspen (*Populus tremuloides*) patches. Clipping experiments demonstrated that the presence of aboveground vegetation reduced survivorship (for birch only), growth (for both species), and nitrogen accumulation (for spruce only) in all patch types. Thus, the understory vegetation in all patch types competed with tree seedlings. However, patch × clipping interactions were either absent or could not explain the greater inhibition of seedling establishment by bluestem or aspen than by horsetail. The strong inhibitory effect of bluestem and aspen on the establishment of spruce and birch seedlings is best explained by the unfavorable temperature and moisture microenvironments in these patches, rather than by differential competition in patches of bluestem, horsetail, or aspen. Many asymmetrical species interactions that are thought to drive successional change may result more from the contrasting effects that species have on their environment than from resource competition among species.

Key words: Alaska; Bonanza Creek LTER; boreal forest; competition; fire; microenvironment; succession; tree seedling establishment; understory vegetation.

Introduction

Successional change in a stand of vegetation is generally a consequence of the interactions among component species and disturbances that disrupt these interactions (Clements 1916, Connell and Slatyer 1977, White 1979). The classic paper of Connell and Slatyer (1977) critically reviewed the literature on plant succession and suggested three models that describe species interactions during succession: (1) facilitation, in which colonizing species make the environment more favorable for later successional species; (2) inhibition, in which initial colonizers competitively inhibit the growth of later successional species; and (3) tolerance, in which initial colonizers have little or no effect on later species. Connell and Slatyer concluded that facilitation may be important in severe environments, as often occurs during early primary succession, that there is little evidence for the tolerance model, and that most successional changes are best explained by the inhi-

bition model, because late-successional species grow better when initial colonizers are removed. More recent studies confirm the importance of positive species effects where the physical environment directly retards plant growth or limits resource supply (Wilson and Agnew 1992, Chapin et al. 1994, Calloway 1995), and of negative species effects in less severe environments (Huston and Smith 1987, Tilman 1988, 1990, Goldberg and Barton 1992, Gurevitch et al. 1992).

The ''negative interactions among species'' invoked in the inhibition model of succession can result from many types of processes (Pickett et al. 1987), including (1) competition for resources (Huston and Smith 1987, Tilman 1990), (2) allelopathy (Wilson and Agnew 1992), (3) modification of the microenvironment (Clements 1916, Connell and Slatyer 1977, Hobbie 1992), and (4) herbivory (apparent competition; Connell 1990). These mechanisms of ''competition'' have received different degrees of emphasis in theoretical treatments of succession, with Clements (1916) and Connell and Slatyer (1977) emphasizing modification of microenvironment, and more recent treatments emphasizing resource competition (Huston and Smith 1987, Tilman 1990). However, there have been few definitive field studies of succession that separate these effects. Reviews of experimental studies indicate that

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interspecific competition is *not* generally stronger than intraspecific competition, suggesting that resource partitioning among species may be less important in explaining species interactions (Goldberg and Barton 1992, Gurevitch et al. 1992) than has been assumed in recent theoretical treatments (Huston and Smith 1987, Tilman 1990). In this paper, we revisit the relative importance of resource competition and microenvironmental modification in a field study of the effects of early-successional colonizers on seedlings of two successionally dominant trees following fire in an Alaskan boreal forest.

Fire is the major disturbance in upland boreal forests. Most interior Alaska forests have burned in the last 200–250 yr (Barney 1971, Viereck 1973), with a fire return time of 50–110 yr in white spruce (*Picea glauca* [Moench] Voss) forests (Yarie 1981), the dominant forest type on south-facing slopes. Site-specific environmental variables (e.g., slope, aspect, elevation, substrate, etc.) affect the assemblage of species after fire (Johnson 1979), and recurrence of fires on a regional scale is affected by climate, landforms, and vegetation (Larsen 1997). Tree establishment occurs mainly in the first few years after a fire (Viereck 1973, Van Cleve et al. 1991). Thus, factors affecting the establishment of tree seedlings during this time are potentially critical to understanding long-term patterns of forest regeneration. These populations may be perpetuated by recurring fires within the life-span of the dominant individuals (Johnson and Fryer 1989).

Competition has been implicated as an important factor that controls the establishment of tree seedlings during succession in most forests (Wilde et al. 1968, Webb et al. 1972, Niering and Goodwin 1974, Harcombe 1977, Van Hulst 1979, Carter et al. 1984), including those in Alaska (Viereck 1973, Walker and Chapin 1986, Wurtz 1988). However, most previous studies of forest succession in Alaska have emphasized the responses of plants to successional changes in the physical environment, particularly soil temperature and nutrients (Van Cleve and Viereck 1983, Van Cleve et al. 1983, 1991).

In this study, we compared the competitive impact of three morphologically distinct colonizing species on the germination and early growth of white spruce, a late-successional tree species, and paper birch (*Betula papyrifera* Marsh.), a midsuccessional tree species. The three colonizing competitor species chosen for study were (1) bluestem (*Calamagrostis canadensis* [Michx.] Beaux.), a grass that forms dense patches and is reported to compete strongly with seedlings of white spruce (Liefers and Stadt 1994); (2) horsetail (*Equisetum arvense* L.), an herbaceous species that forms a short, sparse canopy; and (3) quaking aspen (*Populus tremuloides* Michx.), a tree that forms a tall, dense canopy of root sprouts after a fire. We chose these three competitor species because they are prominent in postfire succession (Viereck 1973), and they differ strikingly in height and density and, therefore, presumably in the type and extent of resource pre-emption. We hypothesized that these three colonizing species would have unequal competitive impacts on tree seedlings and, therefore, that they might influence the density and pattern of forest trees. Alternatively, we considered the hypothesis that successional change after a fire in the boreal forest may be driven more by indirect environmental effects, which are created by early-successional species, rather than by resource competition between early- and later successional species.

METHODS

Study site

The study was conducted from 1988 to 1990 in the Bonanza Creek Experimental Forest (64°45′ N, 148°20′ W) near Fairbanks, Alaska, USA, as part of the boreal forest Long-Term Ecological Research (LTER) Program. The study site (LTER site #UP1a) was located on a south-facing slope in what had been a 170-yr-old white spruce stand (Foote and Viereck 1985) before burning in June 1983 (5 yr prior to this study) in a 3500-ha wildfire (Juday 1985). The site was moderately burned overall, with patches of severe burn, resulting in a mosaic of organic and mineral-soil seedbed (Viereck and Schandelmeier 1980, Foote and Viereck 1985). At the study site, most seedlings were established on ash or thin (< 2.5 cm thick) organic seedbeds (Zasada 1985). Paper birch seedlings also were present. Tree establishment is dependent on trees surviving nearby to supply seeds, as well as on any seeds not destroyed in the fire.

As in other postfire sites of white spruce (Viereck 1973, Van Cleve and Viereck 1983), the mosaic nature of burn severity in the study area resulted in a shrub/herb layer that was dominated by nearly monospecific patches (1–10 m diameter) of bluestem or aspen that had regenerated from belowground organs after the fire (Viereck and Foote 1985). Intermixed with the bluestem and aspen patches were patches of horsetail that contained scattered individuals of fireweed (*Epilobium angustifolium* L.), bluebells (*Mertensia paniculata* [Ait.] G. Don), raspberry (*Rubus idaeus* L.), and wild rose (*Rosa acicularis* Lindl.). The moss *Ceratodon purpureus* (Hedw.) Brid. and the liverwort *Marchantia polymorpha* L. were common. The shrub/herb stage usually lasts ~25 yr, until deciduous trees (paper birch or quaking aspen) become dominant, with white spruce saplings present in the understory. White spruce dominates after ~100 yr (Van Cleve and Viereck 1981, 1983).

The climate of the region is continental, with a growing season limited to ~100 d by late-spring and early-fall frosts (Barney and Berglund 1973). The monthly precipitation (recorded within 1 km of the experimental plots at the LTER1 weather station) from May to August was 47 ± 20 mm (all values mean $\pm$ 1 SE) in

1988, 41 ± 19 mm in 1989, and 82 ± 24 mm in 1990; the 10-yr (1988–1997) mean monthly precipitation was 44 ± 5 mm (L. Viereck, USFS, Fairbanks, Alaska, *unpublished data*).

Natural seedling distributions

To measure natural patterns of establishment of spruce and birch seedlings in relation to understory vegetation, we established a series of parallel 2 m wide transects (spruce seedlings, $n = 30$ transects in 1989; birch seedlings, $n = 10$ in 1990). These transects extended down a broad slope into the burn from a mixed stand of unburned spruce and birch on a ridgetop at one edge of the burn. The spruce transects were 90 m long, resulting in a sampled area of 5520 m². The birch transects were 60 m long and sampled 1080 m² of the same area. We counted spruce and birch seedlings >1 yr old along each transect line and recorded the dominant species of vegetation (patch type: bluestem, aspen, or horsetail) within 25 cm of each seedling. We visually estimated the percent cover for all species in a 1-m² quadrat every 10 m along the transect line in 1989 and every 5 m along the transect in 1990. To determine if the observed density of wild seedlings was greater or lower than expected for each patch type, we normalized seedling density to account for percent cover of each patch type (Neu et al. 1974). We calculated the expected seedling density in a patch type as the average seedling density on a transect × the percent cover of that patch type on that transect. Most seedlings that we aged had become established by 1984, 1 yr after the fire, when only a sparse vegetative cover was present (Viereck and Foote 1985).

We counted the number of adult spruce trees that had been present before the fire (standing logs or stumps) along two parallel transects (300 m long × 50 m wide each) on broad slopes where bluestem patches were uncommon and along two 300 m long × 50 m wide transects in gentle swales where bluestem patches were abundant both before and after the fire. We hypothesized that the abundance of adult trees would be lower in the grass-dominated swales (Gurevitch 1986).

Germination and initial establishment

We used a phytometer approach (Goldberg 1987, Goldberg and Barton 1992) to study the effect of neighbor competition on the germination and initial establishment of spruce and birch. Three types of vegetation patches that were dominated by a single competitor species (bluestem, horsetail, or aspen) were chosen, with 15 replicate blocks of each patch of vegetation. Patches that were selected were ≥7 m in diameter and had >90% cover of the dominant species. In the center of each patch, a 4.1 × 4.5 m plot was established. All aboveground vegetation was clipped and removed from half of each plot every 1–2 wk during the 1988 growing season (clipped treatment); the adjacent half of the plot was the unclipped treatment. There was little regrowth

in 1989 and 1990, and plots were reclipped three and two times, respectively.

In early June 1988, we established six 20 × 20 cm germination plots in both the clipped and unclipped halves of each plot. Germination plots were >10 cm apart and were ≥ 0.9 m from the plot boundaries. We randomly assigned two replicate germination plots to each of the following treatments: control, seeded, and scarified + seeded. We scraped each scarified plot twice in perpendicular directions with a three-toothed trowel to create an organic and mineral-soil seedbed. The scarification treatment was included because studies of natural regeneration of white spruce have shown that exposure of mineral soil facilitates the germination and establishment of seedlings (Dobbs 1972, Putnam and Zasada 1986, Walker et al. 1986).

Control plots were left untreated and were monitored for germination of seeds from natural seed rain. One seeded (unscarified) and one scarified + seeded germination plot in both clipping treatments were selected randomly and were sown with 404 viable white spruce seeds/plot (10 100 seeds/m²); the other seeded and scarified + seeded germination plots each received 140 viable paper birch seeds/plot (3500 seeds/m²). Sowing rates were based on field germination and survival rates of Walker et al. (1986). White spruce seeds had been collected adjacent to the burn area in 1983 and 1984 by the Alaska State Forest Nursery; paper birch seeds had been collected in 1987 from a paper birch forest 28 km northeast of the study site. Seeds were cleaned and stored at $-10°C$ until sown. Germination tests were conducted at 20°C to determine the percentage of viable seeds (white spruce 80%, paper birch 95%).

Germinants were counted in each germination plot at least monthly in 1988 and four times during 1989. No naturally regenerating seedlings were found in the control plots. The maximal number of germinants counted in each plot was used as a measure of germination. In mid-August 1989, we harvested all live germinants in each plot and measured aboveground height and root length of 10 randomly selected germinants; if fewer than 10 survived, all were measured. Germinants were separated into roots, stems, and leaves and were dried to constant mass at 70°C. Prior to statistical analysis, data for each germination plot were pooled.

Transplant experiment

White spruce seedlings were grown for 1 yr in a greenhouse at the Alaska State Forest Nursery in Palmer, Alaska, from seeds collected adjacent to the burned area in 1983. Seeds were sown in May 1986 in a 1:1 medium of *Sphagnum* peat moss and coarse vermiculite in 1000-cm³ cones, and were watered as necessary with soluble fertilizer (NPK 9:45:15 for the first 4 wk and NPK 20:20:20 thereafter). Natural light was supplemented (430 lux; 16-h photoperiod) until the natural photoperiod exceeded 16 h. Greenhouse temperatures

were $20° \pm 2°C$. In July 1987, the seedlings were placed outside to harden for the winter. The following June, these seedlings were transported to Fairbanks and were acclimatized in the shade for 10 d. In early July 1988, four seedlings were transplanted into both clipped and unclipped subplots of each plot. Within each subplot, seedlings were ≥ 25 cm apart and were located ≥ 0.9 m from the subplot's boundaries and from the seed-sowing experiment. Those seedlings that died ≤ 1 mo after transplanting (24% of all seedlings) were replaced.

Locally collected paper birch seeds were sown in the Palmer greenhouse in May 1988 and were grown in 440-cm^3 cones under the same conditions as the spruce seedlings. In early August, four seedlings were transplanted into both clipped and unclipped subplots of each plot, as described for the white spruce. Extra birch seedlings were not, however, available to replace ones that died (29%) following transplant.

For both species, stem diameter at 1 cm and overall height were measured in August 1988 and August 1989, at which time the birch seedlings were harvested (after 1 yr of growth in the field) by clipping the stems at the ground surface. Measurements were repeated for spruce seedlings in September 1990 (after 2.5 yr of growth in the field). We harvested aboveground parts of all spruce seedlings and the roots of one seedling per subplot. Increase in diameter and height were calculated for each seedling as the difference between initial and final measurements. The total leaf area of each birch seedling was measured with a LI-COR LI3000 leaf-area meter (LI-COR, Lincoln, Nebraska, USA). Seedlings from each subplot were separated into old biomass and the current year's biomass (and roots, in the case of spruce) and were dried to constant mass at 70°C. Relative growth rate (RGR) was calculated as (ln[total dry mass] − ln[current year's growth])/1 yr. Prior to statistical analyses, individual masses from a given subplot were pooled. We harvested browsed seedlings in each subplot, but excluded them from the analyses of biomass and allocation.

After weighing, the current year's growth of one unbrowsed seedling was selected randomly from a given sublot and was ground in a Wiley mill (with 20-mesh screen), reground to a fine powder in a ball mill, and analyzed for N with a Carlo Erba C/N analyzer (Carlo Erba, CE Instruments, Milan, Italy). We analyzed N for one seedling from five replicate patches of both clipping treatments within each patch type and calculated N uptake, i.e., [N] × the current year's biomass.

Vegetation and site characteristics

In mid-August 1989, we quantified the amount of aboveground biomass of natural vegetation in each patch type by harvesting at ground level all biomass in a 0.25-m^2 quadrat that was located 1 m inside each unclipped subplot and ≥ 1 m from transplanted spruce seedlings. Samples were oven-dried to constant mass

at 70°C. Belowground biomass was measured in three randomly located 6.4 cm diameter soil cores in five subplots per patch type (one core per subplot in aspen). Each core contained the organic soil layer and the upper 10 cm of mineral soil (i.e., the rooting depth of transplanted seedlings). Roots were separated from soil using a 0.5-mm mesh sieve and were oven-dried to a constant mass at 70°C. Prior to statistical analyses, data from all cores from each subplot were pooled.

To measure the effects of the clipping treatment and to quantify environmental differences among patch types, we measured several abiotic variables. We measured soil temperature at 10 cm depth in each subplot every 2 wk during June–August 1989. We measured soil moisture ≥ 10 d after a rainfall four times in 1989 by coring (10 cm diameter) the organic layer and the top 5 cm of mineral soil. For each sample, we recorded the depth of the organic layer and calculated soil moisture (percentage dry mass after oven-drying the organic horizon to constant mass at 70°C and the mineral horizon at 110°C) and bulk density of each soil layer. On a sunny day (28 July 1989) and a cloudy day (21 September 1990), we measured total photosynthetically active radiation (PAR; 400–700 nm) at ground level within 1 h of solar noon (1300 Alaska Standard Time) in the unclipped vegetation of each patch with a LI-COR (LI-185) radiometer (LI-COR, Lincoln, Nebraska, USA).

Statistical analyses

We conducted three-way ANOVAs (Zar 1984, SPSS 1995) of the percentage germination and survivorship from sown seed in the three treatment combinations, which included the effects of patch type (bluestem, horsetail, aspen) × competition (unclipped [control], clipped) × scarification (unscarified [control], scarified). Percentages of germination and survivorship failed to meet the assumptions of normality (i.e., homoscedasticity, using Levene's test; SPSS 1995), even after standard transformations (arcsine, $1/[X + 1]$; Zar 1984); thus, percentages were rank-transformed (Conover and Iman 1981). Prior to statistical analyses, size-related measurements in both experiments were ln-transformed so that we could interpret interactions as a proportional effect of Species A on Species B. It is considered that ln transformation best represents the way that competition works (Wootton 1994). When ln transformations did not normalize data (using Levene's test), ANOVAs were repeated with ranked data. To test for effects of intraspecific competition on size-related measurements in the seed sowing experiment, we used ANCOVA, with the number of surviving seedlings in each seed plot at the time of harvest as a covariate.

For the transplant experiment, ln-transformed values for biomass, leader length (spruce) or total height (birch), RGR, and leaf area (birch) were analyzed using two-way ANOVA. Vegetation and site characteristics, which included above- and belowground biomass of
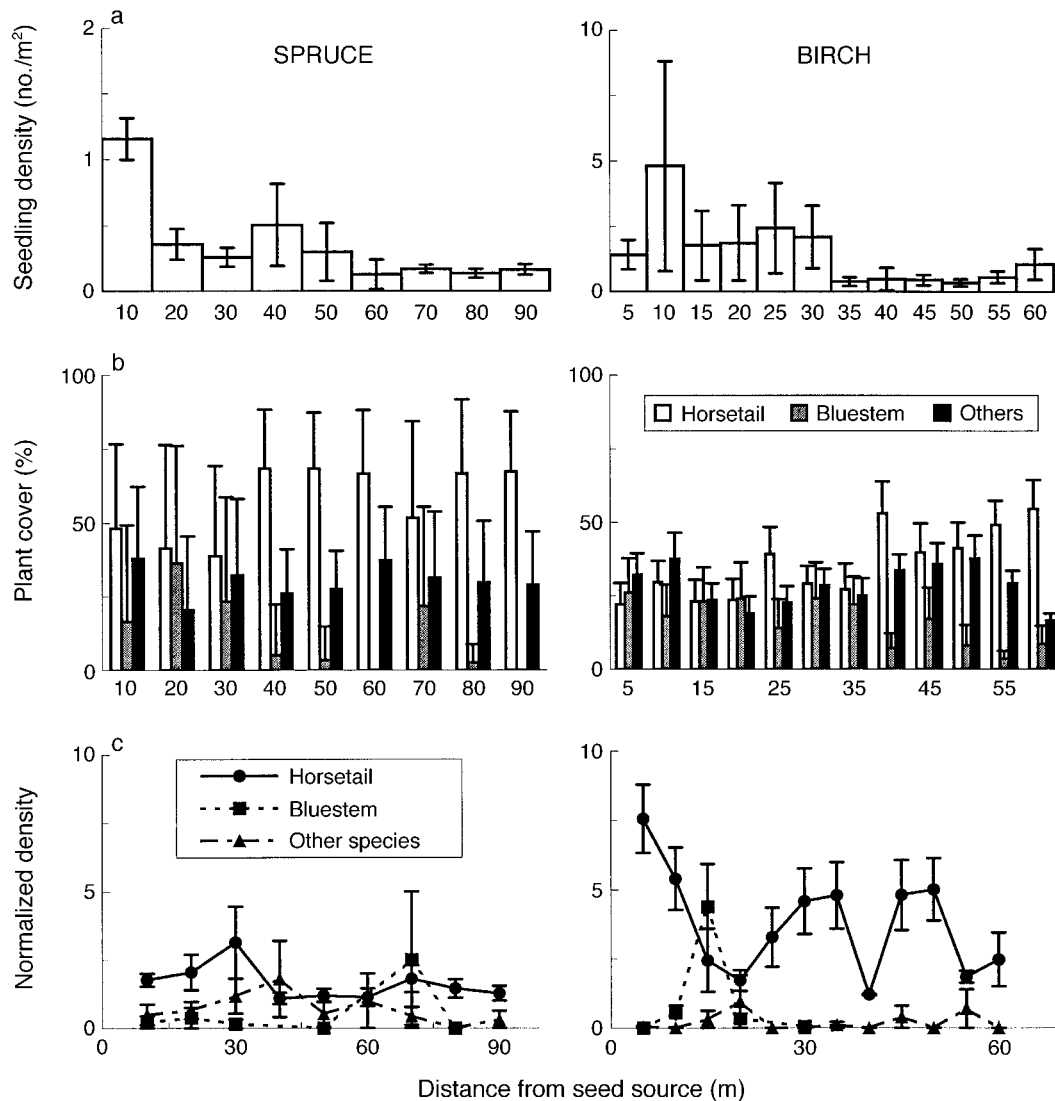
FIG. 1. Effects of distance from seed source on (a) density of naturally occurring white spruce and paper birch seedlings >1 yr old; (b) distribution, by percent cover, of patches of bluestem, horsetail, and all other vegetation; and (c) normalized index of seedling density within patches. The normalized index was calculated by dividing the observed seedling distribution by the expected distribution. Normalized densities >1 indicate preferential establishment in association with the competing vegetation. Data are means ± 1 SE.

natural vegetation, soil moisture, depth of the organic mat, and light attenuation, were also analyzed with two-way ANOVA.

We used Tukey hsd tests for multiple comparisons. We used the Bonferonni technique to control the familywide error rate (FER) at the 5% level (Day and Quinn 1989). Thus, three-way ANOVA results were considered significant for $\alpha < 0.007$ (0.05/7), which accounted for the $n = 7$ comparisons; two-way ANOVA results were considered significant for $\alpha < 0.017$ (0.05/3).

RESULTS

Natural seedling distributions

The density of naturally occurring spruce and birch seedlings decreased exponentially with distance from the seed source (Fig. 1a), similar to the pattern of white spruce seed rain documented in the same site following the 1983 burn (Zasada 1985). Ninety-two percent of the naturally occurring spruce seedlings ($n = 1167$) and 94% of the birch seedlings ($n = 1775$) occurred in horsetail patches. The distribution of seedlings after the fire partly reflects the greater abundance of horsetail patches in the sampled area (Fig 1b). After normalizing seedling density to include percent cover estimates of horsetail, bluestem, and other species, spruce and birch seedlings were found much more often than expected in horsetail patches and much less often than expected in bluestem and other patch types (Fig. 1c). The absence of aspen from the transects prevented us from
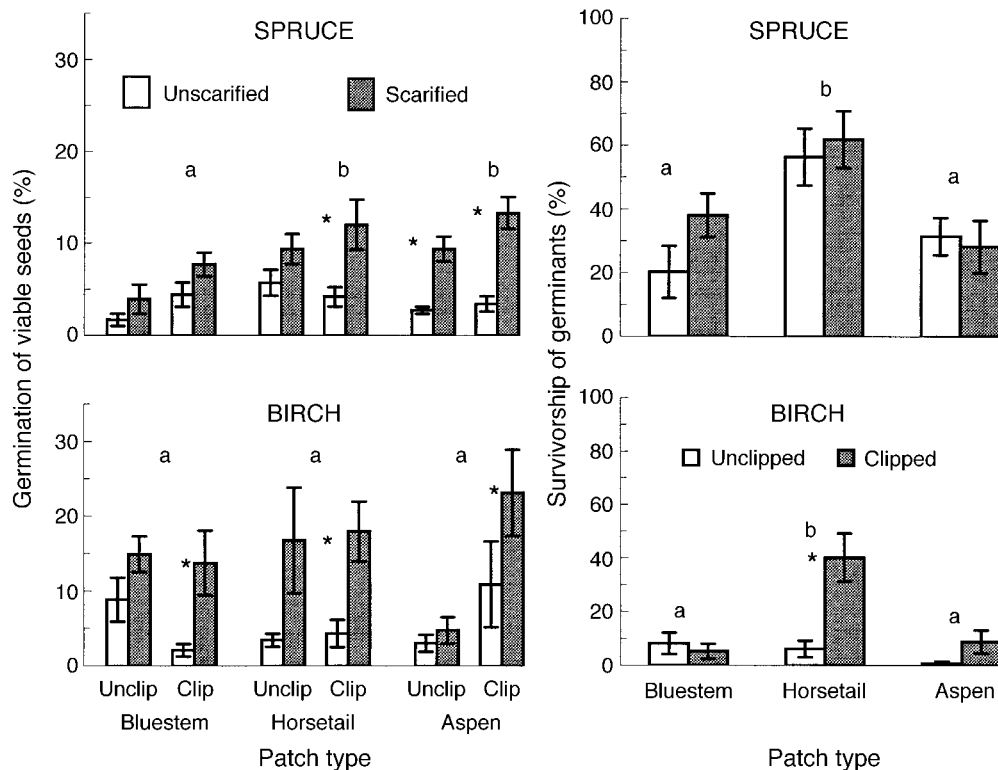
FIG. 2. Germination and survivorship of spruce and birch sown into patches of bluestem, horsetail, or aspen. Within each patch, vegetation was removed (clipped) from half of the plot, and seeds were sown on scarified and unscarified seedbeds. There were no significant effects or interactions of clipping on germination (except for birch germination in aspen), or of scarification on survivorship (Table 1). Data are means ± 1 SE; $n = 15$ patches. Patch types with the same letter are not significantly different ($P \geq 0.05$). Significant differences are starred for scarification treatments (germination) and for clipping treatments (survivorship).

evaluating the effect of aspen on the density of naturally occurring spruce seedlings. The mean density (± 1 SE) of adult white spruce before the fire was nearly twice as high on broad slopes (240 ± 55 trees/ha), where there were fewer patches of bluestem (T.C. Cater and F.S. Chapin, *personal observation*), than in swales (128 ± 10 trees/ha), where bluestem patches were common. These observations indicate that there is a negative relationship between white spruce seedlings and bluestem patches. This negative relationship could contribute to the low density of adult spruce in habitats such as swales, where bluestem is abundant.

Seed sowing experiment

Spruce germination was lower (family-wide error rate <0.05 in all statistical comparisons mentioned in the text) in bluestem than in horsetail and aspen patches, and spruce survivorship was lower in bluestem and aspen than in horsetail (Fig. 2, Table 1), indicating that bluestem and aspen patches were unfavorable for the initial establishment of spruce seedlings. Although birch germination was unaffected by patch type, birch survivorship also was lower in bluestem and aspen than in horsetail. Scarification increased the germination rate of both species (Table 1), but did not overcome

the reduced spruce germination in bluestem patches (Fig. 2). The removal of aboveground vegetation did not significantly affect germination or survivorship of either species (Table 1), except for increased birch germination in clipped aspen patches and increased birch survivorship in clipped horsetail patches.

Both the biomass and the total length (shoot height + root length) of spruce germinants were greater when sown in horsetail than in bluestem or aspen patches (Fig. 3, Table 1). In contrast, total biomass and length of birch germinants were not greater in horsetail than in the other patch types. The significant effect of clipping on the growth of both spruce and birch germinants (Fig. 3, Table 1) indicates that aboveground competition strongly inhibited initial seedling growth. Further, the absence of a patch × clipping interaction suggests that the three patch types had a similar competitive impact on germinants. The total number of surviving spruce germinants was a significant covariate in the total length analysis for spruce germinants (Table 1), suggesting that intraspecific competition also inhibited initial seedling growth. No treatment significantly affected allocation (root:shoot ratio) of spruce or birch, and scarification had no effect on the survivorship or growth of spruce or birch (Table 1). In summary, horse-

TABLE 1. Probability values (from *F* tests) from ANOVAs testing the germination and survivorship of spruce and birch seeds that were sown in the combinations of three patch types (PT), two clipping (CL) treatments, and two scarification (SC) treatments.

Dependent variable	Trans-forma-tion	Treatment			Interactions				No. survi-vors
		PT	CL	SC	PT × CL	PT × SC	CL × SC	PT × CL × SC	
Spruce									
Germination (% viable seeds)	rank	**<0.001**	0.012	**<0.001**	0.010	0.030	0.178	0.976	
Survivorship (% germinants)	rank	**<0.001**	0.112	0.379	0.072	0.228	0.635	0.936	
Root + shoot length (cm)	ln	**<0.001**	**0.005**	0.210	0.033	0.560	0.106	0.446	**0.003**
	rank	**<0.001**	**0.008**	0.233	0.121	0.661	0.185	0.280	**0.001**
Biomass (g/seedling)	ln	**<0.001**	**<0.001**	0.403	0.089	0.361	0.288	0.383	0.110
	rank	**<0.001**	**<0.001**	0.341	0.548	0.351	0.292	0.276	0.033
Root : shoot ratio	ln	0.537	0.179	0.118	0.148	0.243	0.298	0.837	0.386
	rank	0.227	0.926	0.322	0.303	0.677	0.194	0.126	0.190
Birch									
Germination (% viable seeds)	rank	0.889	0.445	**<0.001**	**<0.001**	0.709	0.071	0.638	
Survivorship (% germinants)	rank	**0.004**	**0.004**	0.659	0.129	0.643	0.525	0.926	
Root + shoot length (cm)	ln	**0.024**	**0.007**	0.383	0.961	0.856	0.223	0.731	0.850
	rank	**0.008**	**0.001**	0.402	0.705	0.998	0.457	0.528	0.937
Biomass (g/seedling)	ln	0.035	**0.007**	0.219	0.767	0.946	0.797	0.786	0.350
	rank	0.011	**0.001**	0.202	0.495	0.928	0.973	0.195	0.182
Root : shoot ratio	ln	0.268	0.634	0.202	0.409	0.526	0.377	0.161	0.654

Notes: The number of survivors was used as a covariate for ANCOVA conducted for growth parameters after germination and two growing seasons. A family-wide error rate of $P = 0.05$ is associated with a probability level of $P = 0.007$, following Bonferroni adjustment. Significant effects of treatments and interactions on the germination and survivorship of spruce and birch are shown in bold, as are significant effects of interspecific competition (i.e., number of surviving seedlings) on growth parameters.

tail patches were favorable to the germination and growth of spruce and birch seedlings, whereas bluestem and aspen patches were unfavorable sites for establishment of spruce and birch seedlings, but this pattern was not explained by patch-related differences in the availability of mineral soil (scarification × patch interactions) or by aboveground competition (clipping × patch interactions). The only exception to this pattern was birch germination, which was enhanced by clipping of aspen.
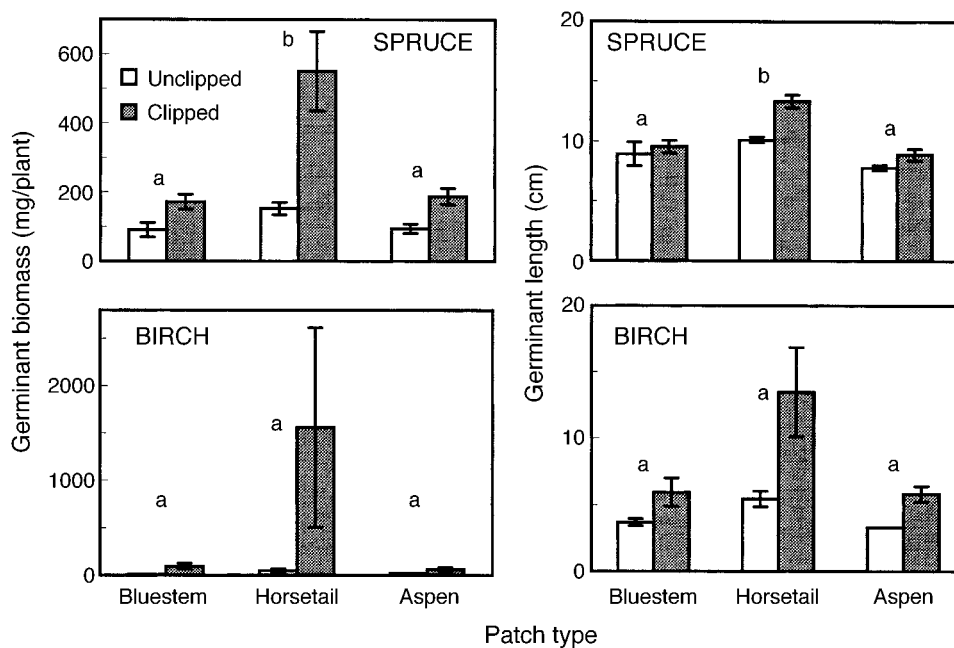

FIG. 3. Biomass and plant length (root + shoot) of spruce and birch germinants in seedbeds in three patch types in the presence or absence (clipped) of aboveground vegetation. Data are means ±1 SE; $n = 15$ patches. Different letters indicate significant differences among patches.
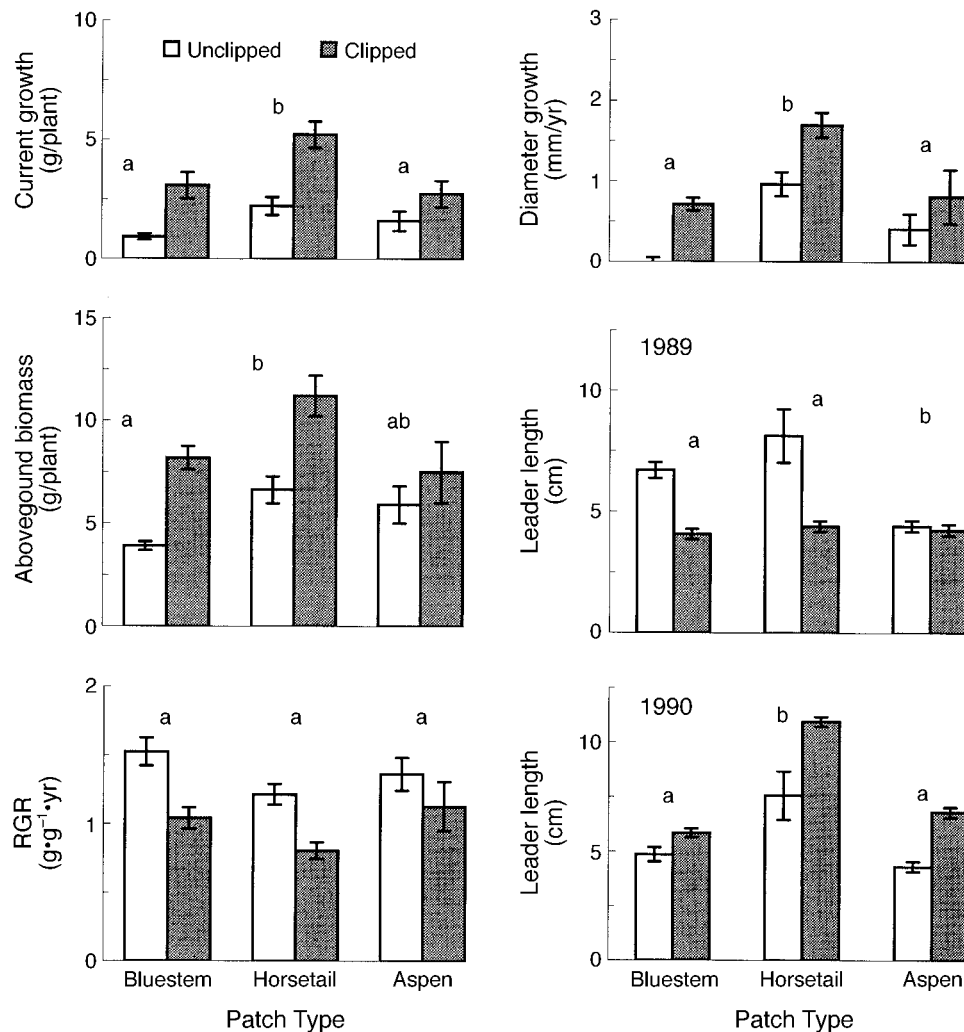
FIG. 4. Growth parameters after two years (1989; leader length only) and after three years (1990) of spruce seedlings transplanted into clipped and unclipped treatments in three patch types. Data are means ±1 SE; $n = 15$ patches. Statistics as are in Fig. 2. Except for the 1989 leader-length panel, all panels are for 1990 data.

Transplant experiment

Spruce seedlings transplanted to the field had more biomass in current-year growth, longer leaders in 1990, and more radial growth in horsetail than in bluestem and aspen patches (Fig. 4, Table 2). Spruce seedlings in horsetail patches also accumulated more aboveground biomass than did seedlings in bluestem patches. In contrast, growth of leaders in 1989 was greater in bluestem and horsetail than in aspen patches. There was no effect of patch type on the root:shoot ratio (Table 2). Horsetail patches also were more favorable for the growth parameters of transplanted birch seedlings than were aspen or bluestem patches, as measured by aboveground and current year's biomass, RGR, basal-stem diameter growth, height growth, and leaf area (Fig. 5, Table 2). There was no treatment effect on any growth parameter in either species at the time of transplant (data not shown), indicating that the growth pat-

terns observed were caused by the treatments and not by pretreatment differences in the three types of vegetation patches.

In aspen patches, most (88%) spruce seedlings were browsed by snowshoe hares (*Lepus americanus*), as indicated by the distinctive diagonal orientation of the clipping. In contrast, fewer seedlings were browsed in bluestem (21%) and horsetail (16%) patches, reflecting the tendency of snowshoe hares to concentrate their activity in sites of dense woody cover (Wolff 1980). Browsing rates on birch seedlings were less frequent (10%, 13%, and 4% in aspen, bluestem, and horsetail, respectively) than those of spruce seedlings.

Clipping aboveground vegetation reduced leader growth of spruce seedlings in 1989 in bluestem and horsetail patches (Fig. 4, Table 2), perhaps by preventing etioloation, but it did increase leader growth in 1990 in all patch types and greatly increased above-

TABLE 2. Probability values (from *F* tests) from ANOVAs that tested the response of transplanted white spruce and paper birch seedlings to the three patch types (PT) and two clipping treatments (CL).

Dependent variable	Trans-form-ation	Spruce			Birch			
		PT	CL	PT × CL	Transfor-mation	PT	CL	PT × CL
Diameter growth (mm/yr)	ln	**<0.001**	**0.001**	0.025	ln	**<0.001**	**<0.001**	0.257
Spruce leader growth, 1989 (cm)	ln	**<0.001**	**<0.001**	**<0.001**				
Spruce leader growth, 1990 (cm)	ln	**<0.001**	**0.010**	0.530				
Total height growth (cm/plant)	ln	**0.010**	0.959	0.859	ln	**<0.001**	0.597	0.382
Leaf area (cm²)	...	...	...	...	ln	**<0.001**	**<0.001**	0.795
Aboveground biomass (g/plant)	ln	**<0.001**	**<0.001**	0.086	ln	**<0.001**	**<0.001**	0.695
Current year's biomass (g/plant)	ln	**<0.001**	**<0.001**	0.144	ln	**<0.001**	**<0.001**	0.688
Root : shoot ratio	none	0.026	0.032	0.887	...	...	...	...
RGR	none	**0.004**	**<0.001**	0.555	none	**<0.001**	0.144	0.793
Tissue N (%)	none	0.381	0.142	0.736	ln	0.022	0.078	0.041
N pool (mg N/seedling)	ln	0.011	**0.001**	0.284	ln	**<0.001**	**0.010**	0.105

Notes: A family-wide error rate of $P = 0.05$ is associated with a critical probability level of $P = 0.017$, following Bonferroni adjustment. Significant treatments and interactions are shown in bold.

ground and current year's biomass and basal-diameter growth. The larger plants in the plots from which competing vegetation was removed had lower RGR, as expected, because RGR decreases with increasing size (Cook and Evans 1983). Removing aboveground vegetation had no effect on root : shoot ratios (Table 2).

The growth of birch transplants also was stimulated by the removal of competing vegetation, as seen in increased aboveground and current year biomass, basal-stem diameter growth, and leaf area (Fig. 5). The lack of significant patch × clipping interactions (except for spruce leader growth in 1989, when clipping had rel-
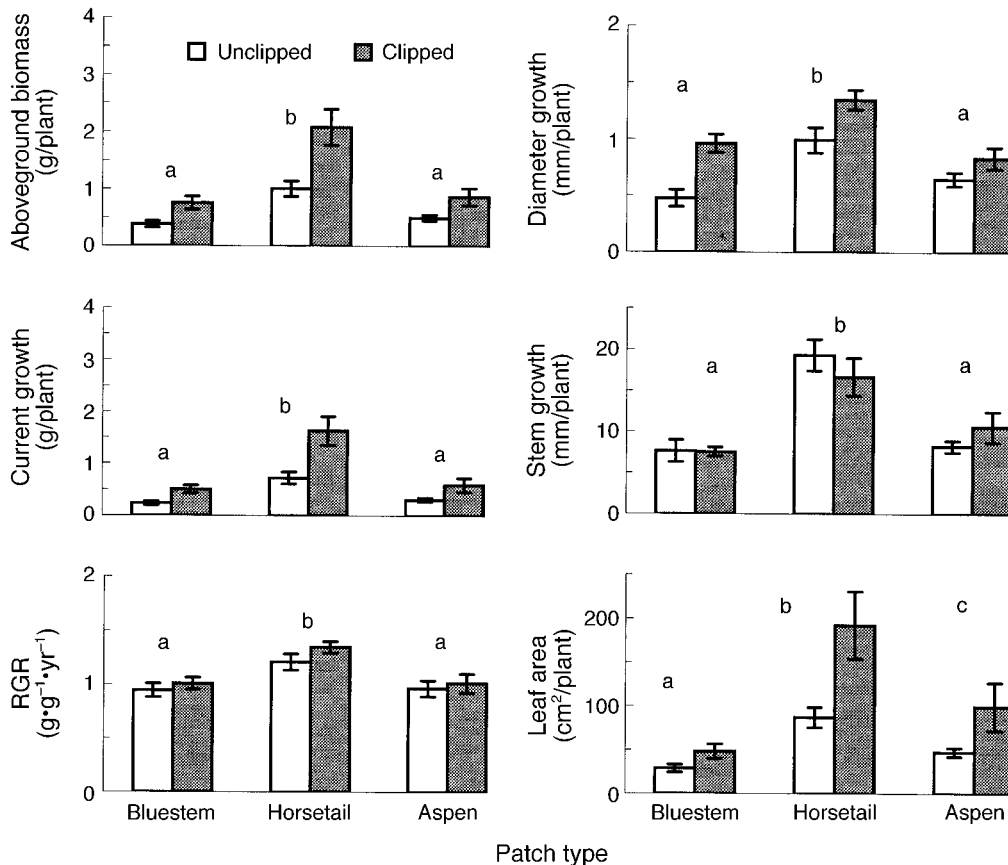

FIG. 5. Growth parameters after one year (1989) of birch seedlings transplanted into clipped and unclipped treatments in three patch types. Data are means ± 1 SE; $n = 15$ patches. Statistics are as in Fig. 2.
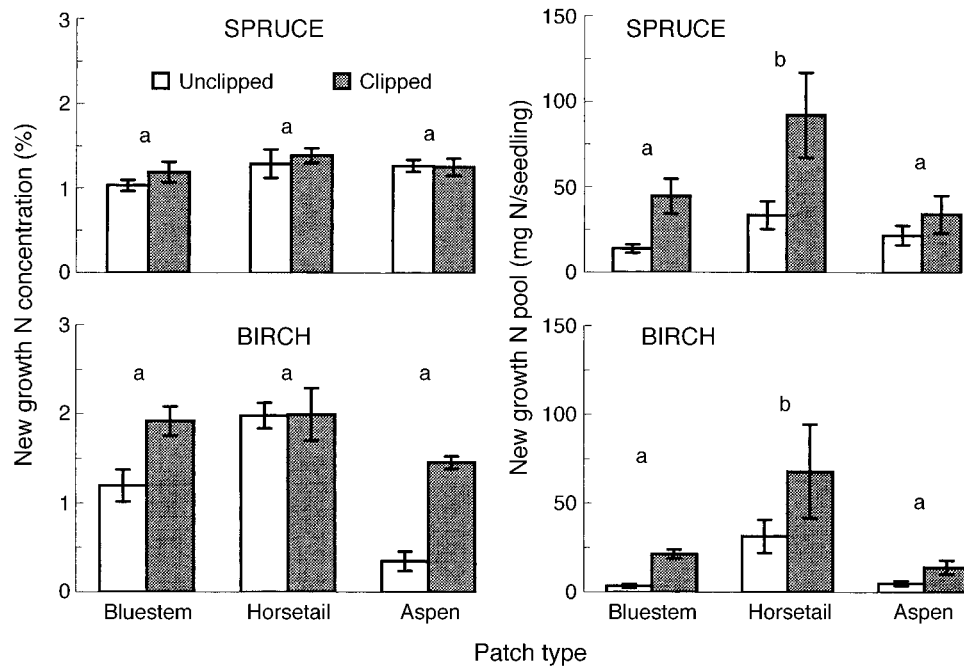
FIG. 6. N concentration in new growth as a percentage of new growth biomass and N uptake (N accumulation in current year's growth) of spruce and birch seedlings transplanted into clipped and unclipped treatments in three patch types. Data are means ±1 SE; $n = 5$ patches. Statistics are as in Fig. 2.
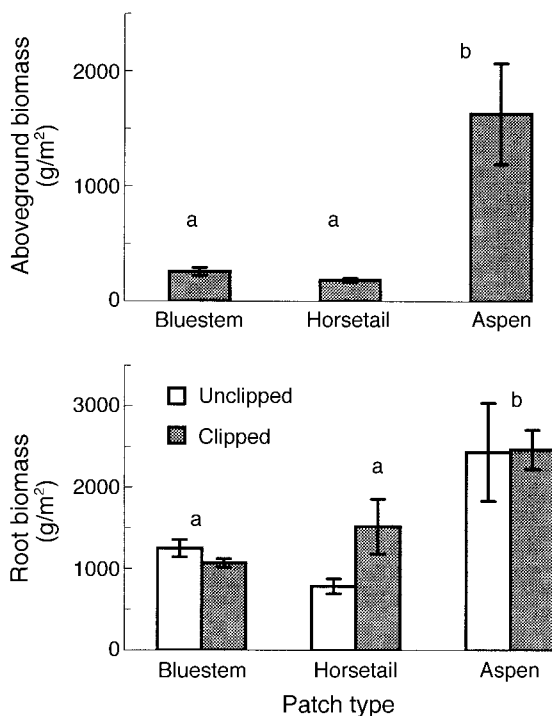

FIG. 7. Aboveground and root biomass of natural vegetation in mid-August 1989 in patches of bluestem, horsetail, and aspen. Data are means ± 1 SE; $n = 13$–14 for aboveground biomass, $n = 5$ for root biomass. Statistics are as in Fig. 2.

atively little effect in aspen) indicates that clipping in the patches of bluestem, aspen, and horsetail patches resulted in similar impacts on the growth of transplanted seedlings.

There was no patch or clipping effect on tissue N concentration of either spruce or birch seedlings (Fig. 6, Table 2), so patterns of N uptake in new (current) growth (Fig. 6) reflected site and treatment differences in biomass of new growth (Fig. 5). Spruce and birch seedlings in horsetail patches accumulated more N in new growth than did seedlings in other patch types, and the removal of competing aboveground vegetation greatly stimulated N accumulation in new growth, particularly in the horsetail and bluestem patches. These results indicate that those patches supporting the greatest growth rates also had greater N absorption, and that the stimulation of growth associated with the removal of competing aboveground vegetation also was associated with greatly increased N absorption.

Vegetation and site characteristics

Aspen had significantly more above- and belowground biomass than did horsetail or bluestem (Fig. 7, Table 3). Bluestem soils were cooler in unclipped treatments (Fig. 8), and the organic horizon was thicker and wetter in bluestem patches than in horsetail and aspen patches (Fig. 9). Soil moisture in the mineral horizon was similar among patch types (Fig. 9), as was bulk density (data not shown). The removal of aboveground vegetation consistently created warmer ($P < 0.05$)

TABLE 3. Probability values (from *F* tests) from ANOVAs performed for vegetation and site characteristics of the three patch types (PT) and two clipping (CL) treatments.

Dependent variable	Trans-forma-tion	PT	CL	PT × CL
Aboveground biomass (g/m²)	rank	**0.002**		
Root biomass (g/m²)	ln	**<0.001**	0.146	0.082
Soil moisture (% dry mass)				
Organic horizon	none	**0.005**	0.686	0.190
Mineral horizon	rank	0.091	0.010	0.187
Organic mat depth (cm)	ln	**<0.001**	0.703	0.712
Light attenuation (% full sun)				
Clear day	rank	0.716	...	...
Cloudy day	rank	**<0.001**	...	...

soils, especially in bluestem patches, but had little effect on soil moisture in either the organic or mineral horizon, the thickness of the organic mat, or bulk density (Table 3). On a sunny day, PAR was attenuated to a similar degree in all patch types (Fig. 10). On a cloudy day, however, aspen and especially bluestem patches attenuated PAR more than did horsetail patches.

DISCUSSION

The preferential establishment of naturally occurring spruce and birch seedlings in patches of horsetail and the relative exclusion of spruce and birch from bluestem patches demonstrate the importance of understory vegetation in determining patterns of postfire tree regeneration. The low density of mature trees in habitats,

FIG. 9. Depth of the organic mat (*n* = 15 patches) in bluestem, horsetail, and aspen patches, and seasonal average soil moisture in the organic mat and in the underlying mineral horizon. Statistics are as in Fig. 2.
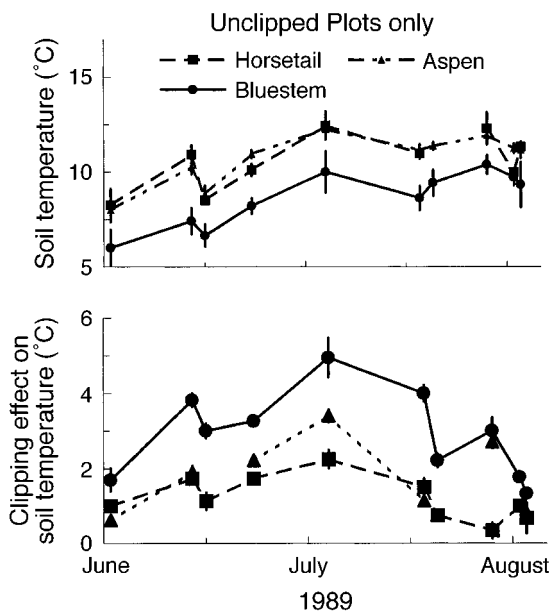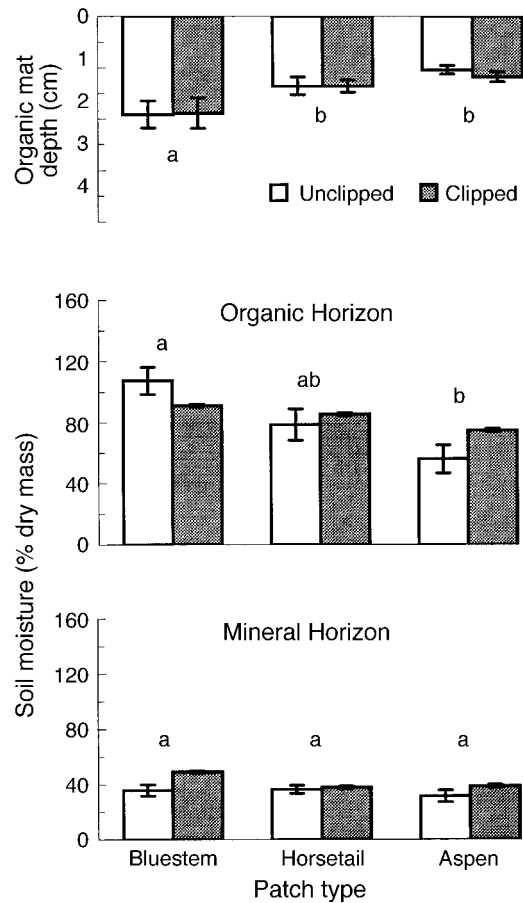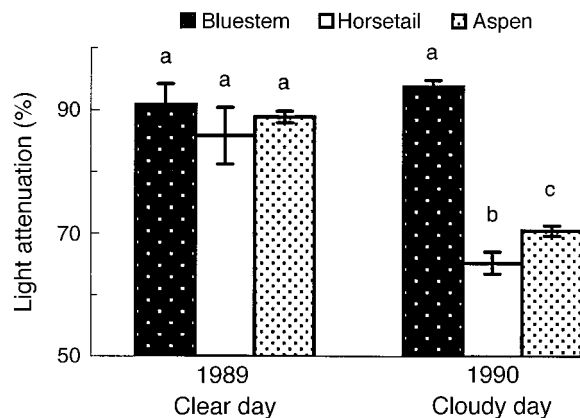

FIG. 8. Seasonal pattern of soil temperature at 10 cm depth in the unclipped treatments in three patch types, and the effect of clipping (clipped minus unclipped [control]) on soil temperature in three patch types. Data are means ± 1 SE; *n* = 15 patches.

FIG. 10. Light attenuation in bluestem, horsetail, and aspen patches on a clear day in 1989 (*n* = 4, 5, and 7 patches, respectively) and on a cloudy day in 1990 (*n* = 27, 33, and 32 patches, respectively). Statistics are as in Fig. 2.

such as swales, that favor bluestem suggest that these patterns of differential establishment in distinct patch types could have long-term consequences for forest structure, although environmental differences between swales and broad slopes could also be important. A similar relationship between seedling density and the distribution of different herb patches occurs in eastern deciduous forests (Maguire and Forman 1983), in old-field succession (Harrison and Werner 1984), and on arctic tundra (Gartner et al. 1986). In boreal forests such as the one that we studied, where the understory vegetation survives and resprouts after fire, the species composition of the understory can strongly influence the pattern of overstory development (Niering and Egler 1955, Niering and Goodwin 1974, Harcombe 1977, Van Hulst 1979, Peet and Christensen 1980, Eis 1981, Walker and Chapin 1986).

Removal of early-successional plants enhanced the nitrogen uptake (for spruce), growth (for spruce and birch), and survivorship (for birch) of later successional tree seedlings, consistent with earlier observations that removal of early-successional vegetation increased basal diameter growth of white spruce seedlings (Wurtz 1988) and that logged sites with dense herbaceous vegetation show little white spruce regeneration (Hogg and Lieffers 1991). These results from the boreal forest support Connell and Slatyer's (1977) conclusion that early-successional species generally inhibit the growth of later successional dominants.

Resource competition was clearly one important mechanism of the inhibition of the later successional species; when early-successional species were removed, tree seedlings acquired more carbon and nitrogen, the two resources most likely to limit seedling growth (Van Cleve et al. 1991). However, there were probably several additional direct and indirect mechanisms by which early-successional vegetation inhibited establishment and growth of tree seedlings (Connell 1990). The increased soil temperature in clipped plots probably augmented seedling N uptake through enhanced N mineralization and N supply (Van Cleve et al. 1983, Van Cleve and Yarie 1986) and through direct temperature effects on N uptake (Chapin and Tryon 1982) and growth (Chapin and Tryon 1983, Lawrence and Oechel 1983), as well as through reduced competition for resources from early-successional species. The improved germination following scarification suggests that the accumulation of organic matter beneath vegetation inhibits germination. Similarly, elsewhere in interior Alaska, white spruce regeneration is greater on mineral than on organic soils (Zasada and Gregory 1969, Dobbs 1972, Putnam 1985, Walker et al. 1986). Most tree seedlings at our site established immediately after the fire, before the accumulation of a surface organic mat. Other potential mechanisms of inhibition by early-successional species include cover for herbivores, as we observed in aspen patches, and allelopathy, which we did not study.

The seed-sowing and transplant experiments demonstrate that horsetail patches were more favorable sites for seedling growth than were bluestem or aspen patches. Whenever there was a significant patch effect, it occurred because seedlings grew best in horsetail patches or grew least well in bluestem patches. The strong inhibition of tree seedling establishment by bluestem is also well documented in other studies (McQuilkin 1940, Waldron 1966, Eis 1981, Pyšek 1993).

Contrary to our initial hypothesis, the general lack of patch × clipping interactions suggests that aboveground competition was not the primary mechanism responsible for the differential establishment of spruce and birch seedlings in different patch types. This result is surprising, given the large differences in biomass, size, and growth form of aspen, bluestem, and horsetail. We might have failed to see patch × clipping interactions because of the relatively low statistical power of our multiple-comparison experimental design. However, when patch × clipping interactions were observed, they generally occurred because plants responded more to vegetation removal in horsetail than to other patch types, i.e., that competitive release was greatest in patch types that were least inhibitory to establishment. Thus, both the statistical analysis and the patterns of response in the data suggest that some factor other than resource competition must account for differential establishment and growth among patch types.

Differences in environment among patch types were sufficient to explain differential establishment, N uptake, and growth of tree seedlings. Bluestem patches were cold and shaded, whereas aspen patches were dry and shaded and had higher rates of browsing. In contrast, horsetail patches were warm and showed the least light attenuation. According to other studies (Uchino et al. 1984) horsetail patches also support rhizosphere nitrogen fixation. These factors would all contribute to the greater N uptake by white spruce seedlings in horsetail patches.

Many studies of plant competition do not test statistically, as we did, whether species differ in their competitive impact on a target species. When these statistical comparisons have been made (Goldberg and Barton 1992), some species differ in their competitive impact on a target species (Miller and Werner 1987, Wilson 1989), but many other species are competitively equivalent (Goldberg and Werner 1983). We suggest that many of the asymmetrical species interactions that are thought to cause the structuring and changes in vegetation (Tilman 1988) may be due more to the differential effects of species on environment or to the association between species and certain microenvironments, rather than to differences in competitive impact among species.

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