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DEVELOPMENTAL PLASTICITY ALLOWS *BETULA NANA* TO DOMINATE TUNDRA SUBJECTED TO AN ALTERED ENVIRONMENT

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Abstract. We investigated how three co-dominant arctic shrubs (*Betula nana, Salix pulchra,* and *Ledum palustre* ssp. *decumbens*) responded to long-term treatment with N+P fertilizers and greenhouses in a factorial field experiment at Toolik Lake, Alaska. Our goal was to understand the relationship between growth of individuals and species abundance in the community, and the mechanism by which one species achieves dominance under changed environmental conditions. We compared aboveground growth and allocation patterns in individual ramets 15 yr of age with community abundance measured by quadrat harvests. Ramets of all three species substantially increased their stem biomass with fertilization, but the increase was much larger for *Betula* than for the other two species. In quadrat sampling, only *Betula* appreciably increased its biomass per unit area with fertilization or greenhouse treatment. For *Salix* in all treatments, and *Ledum* in the two fertilizer treatments, ramet density per unit area decreased more than growth of surviving 15-yr-old ramets was promoted, so community biomass of these species declined. In contrast, *Betula* increased its ramet density in all treatments by producing new shoots from stems older than 15 yr, even though stem mortality was also increased in the two fertilizer treatments.

Betula increased its growth in part by a major change in allocation, from producing mostly short shoots to producing many more long shoots. As a result, the number of branches and the rate of production of new meristems greatly increased. This developmental plasticity allowed extensive growth that led to development of a dense canopy and imposed light limitation on the other species. The flexible growth strategy of *Betula* points to the importance of meristem availability and developmental constraints in determining plant response to environmental change. Developmental controls over meristem availability are not usually considered in ecological paradigms for allocation, but they may be useful for predicting plant response to changes in nutrient availability in other ecosystems.

Key words: Betula nana; *clonal growth; elevated temperature;* Ledum palustre; *meristem limitation; nitrogen; phosphorus;* Salix pulchra; *tundra.*

Introduction

Plant development affects the form and function of individual plants through its control over plant architecture, allocation, and the timing of growth. Development controls the expression of phenotypic plasticity in response to environmental conditions (Diggle 1994, Pigliucci 1997, Pigliucci et al. 1997). Developmental processes may affect ecosystem processes, if differences in developmental patterns between plants affect vegetation response to disturbance or changing environmental conditions. Although in most work on plant response to changing conditions, development has not been considered explicitly, developmental processes have been implicated in controlling vegetation response to herbivory and plant resource acquisition (e.g., Coleman and Jones 1991, Jones et al. 1993, Coleman et al. 1994, Ruohomäki et al. 1997). Better understanding of how and when plant development is important to ecosystem response to changing environmental conditions requires direct comparison between an individual species' growth response and how its abundance changes in the community.

Previous long-term experiments altering nutrient availability and temperature in arctic tundra changed ecosystem properties, such as species and growth-form composition, nitrogen cycling, and net primary production (Chapin et al. 1995), and also changed the growth of individual species (Chapin and Shaver 1996). In order to compare long-term patterns of growth and allocation in individual ramets with community abundance of three tundra shrub species, we repeated this experiment. Our objectives were (1) to quantify and compare individual growth and development with species abundance in the community, (2) to understand how one species could achieve dominance, and (3) to identify factors that control plant response to environmental change in this ecosystem. From results presented here, we suggest that developmental differences

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between species in the numbers of active meristems available for vegetative growth may constrain plant response to altered environmental conditions and thus affect the community's response.

METHODS

Site and treatments

We conducted the study in moist tussock tundra (Bliss and Matveyeva 1992) near Toolik Lake at the arctic Long Term Ecological Research (LTER) site in the northern foothills of the Brooks Range, Alaska (68° 38′ N, 149° 34′ W, elevation 760 m). Vegetation there is composed of approximately equal biomass of graminoids (mainly *Eriophorum vaginatum* and *Carex bigelowii*), deciduous shrubs (mainly *Betula nana, Salix pulchra,* and *Rubus chamaemorus*), evergreen shrubs (mainly *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea*), and mosses (mainly *Sphagnum* spp., *Hylocomium splendens,* and *Aulacomnium turgidum*) (Shaver and Chapin 1991). Nomenclature follows Hultén (1968).

In 1988, we established four replicate blocks in homogeneous tussock tundra on a gentle (5%), north-facing slope, each block containing 10 5 × 20 m plots separated by 2-m buffer strips, following an experimental design previously employed (Shaver and Chapin 1980, Chapin and Shaver 1985, Shaver et al. 1991, Chapin et al. 1995, Chapin and Shaver 1996). Within each block, three plots were randomly assigned to the following treatments: (1) control (no manipulation), (2) fertilization with N and P, (3a) greenhouse treatment to elevate air and soil temperatures during the growing season, and (3b) fertilizer plus greenhouse treatment. The two greenhouse treatments were located on the same plot, with the fertilized greenhouse placed at least 2 m down the slope from the unfertilized one. This ensured that the unfertilized greenhouse was not affected by leaching of nutrients from the fertilized greenhouse. The remaining seven plots in each block received other treatments (e.g., shading, shading plus (N+P) fertilizers, N alone, P alone), results of which are not included in the present report.

Although both the fertilized and unfertilized greenhouses were located on the same plots, these treatments were considered independent in the factorial analysis of results. Extensive previous experience with these manipulations in moist tussock tundra vegetation at Toolik Lake and elsewhere (Shaver and Chapin 1986, Chapin et al. 1995, Shaver and Chapin 1995) indicates that the minimum 2 m distance between greenhouses is more than sufficient to isolate these treatments from one another. In support of this, we found no significant greenhouse × fertilizer interactions in statistical analyses of results from this study.

For all fertilization treatments, we used the same N and P fertilizers and application methods as in previous work (Shaver and Chapin 1980, Shaver et al. 1986, Chapin et al. 1995, Chapin and Shaver 1996). N and P were applied to the fertilized plots annually in late May or early June, starting in 1989. We applied N (as slow-release granular ammonium nitrate) at 10 $g \cdot m^{-2} \cdot yr^{-1}$ and P (as granular superphosphate) at 10 $g \cdot m^{-2} \cdot yr^{-1}$ in the first year and 5 $g \cdot m^{-2} \cdot yr^{-1}$ in subsequent years.

Greenhouses, first put in place in June of 1989, had permanent, rectangular (2.46 × 4.92 m), wooden frames with a gable roof 65 cm above the ground at the sides and 130 cm at the center line. Roof and all four sides were covered with transparent 0.15-mm (6-mil) UV-resistant clear polyethylene sheeting (Cloud 9 commercial greenhouse plastic; Monsanto, Incorporated, St. Louis, Missouri). Greenhouse frames remained in place year round, but the plastic was put in place at the beginning (25 May–5 June), and removed at the end (20–25 August), of each growing season.

Environmental monitoring

Beginning in 1990, in one control and one greenhouse plot, we measured intensity of photosynthetically active radiation (PAR, measured as micromoles of photons per square meter per second; 400–700 nm, Quantum sensor Li 190SB; LiCor Incorporated, Lincoln, Nebraska), air temperature and relative humidity (Model 207 temperature and relative humidity probe; Campbell Scientific, Logan, Utah), and soil temperatures (copper-constantan thermocouples; Omega Engineering, Incorporated, Stamford, Connecticut). Wind speed and direction (Met-One probe; Campbell Scientific, Logan, Utah) were also recorded at 3 m above the ground in the control plot only. Values were continuously recorded with a datalogger (CR21X; Campbell Scientific, Incorporated, Logan, Utah). PAR intensity was recorded in both treatments at 65 cm above the ground, which was above the vegetation. Air temperature and relative humidity were recorded 1 m above the ground in both greenhouse and control plots and in control plots also at 3 m, which is the standard height for these measurements at LTER sites. Soil temperature was measured at 0, 10, 20, and 40 cm below the surface. Measurements were made each minute, with hourly averages and daily means recorded by the datalogger. Growing degree-days were calculated by summing the mean daily temperatures of all days with mean air temperature > 0°C, excluding days with mean air temperature < 0°C. Thaw depth was measured in all treatments in August of 1993 and 1997 by pushing a thin metal probe from the moss surface to the bottom of the thawed soil in eight intertussock areas per plot.

Growth history of individual ramets

To compare growth of individual plants with their abundance in the community, in the summer of 1995 we analyzed branches from two deciduous (*Betula nana, Salix pulchra*) and one evergreen (*Ledum palustre* ssp. *decumbens*) shrub species for growth prior

to and during the experiment (the most apical 12–15 yr of growth). These shrubs are long lived and grow clonally; their supporting branches are largely prostrate and become progressively covered by moss, after which they produce adventitious roots. It is thus difficult to identify genetic individuals. Three individual ramets (large, rooted branches) of each species were chosen randomly from each treatment in each block (a total of 12 ramets per treatment except for *Salix* in the greenhouse plus fertilizer treatment). Ramets were sampled from one half of the plot, leaving the other half undisturbed for determinations of aboveground biomass in the community (see *Aboveground biomass harvests*, below). In the greenhouse plus fertilizer treatment, there were only enough stems of *Salix* in the sampled part of the plot to obtain one ramet from each of three blocks. Ramets were harvested sequentially from mid-June to early August. We analyzed one ramet of each species from all treatments in all blocks, before continuing on to the second and third ramets.

Detailed information on age structure within these ramets will be presented and methods described elsewhere. Briefly, branch ages in ramets of *Salix* and *Ledum* were determined by counting terminal bud scars (Shaver 1986), which are visibly persistent for many years. *Betula* does not form persistent bud scars. Branch ages in *Betula* ramets were determined by cutting thin stem cross sections at various points in the ramet by hand with a razor blade, staining them with 1% phloroglucinol in 20% HCl, and counting annual growth rings at 60× or 100× magnification under a compound microscope.

Betula makes two types of shoots, long shoots and short shoots. Long shoots undergo extensive primary and secondary growth. Short shoots elongate < 2 mm per year and have almost undetectable secondary growth. Short shoots occasionally convert into long shoots, after which they undergo secondary growth as other long shoots do. We define the term ''structural branch'' for *Betula* to include only long shoots and former short shoots that have converted to become long shoots. Short shoots do not form clear growth rings, so our estimates of their age are maximum estimates, one year less than the age of the structural branch to which they are attached. For *Salix* and *Ledum* all branches are structural, as these plants do not make short shoots.

Branch segments were dried at 65°C for 48 h and weighed, separating short shoots, converted short shoots, and long shoots of *Betula*. Branch numbers and masses were averaged among the three ramets per plot, then among the four blocks for each treatment. All values are presented as means ± 1 SE, using standard errors for the means among blocks ($n = 4$). Data on the current year's shoots are not included here, because their mass increased substantially between successive ramet sampling times.

Dead branches of ramets

To estimate mortality within ramets, the number of dead structural branches attached to each ramet was counted. For *Salix* and *Ledum*, this was the total number of branch tips in all dead branch systems attached to living stems. In *Salix*, death of a shoot from a terminal bud was not counted if that shoot had less than one year of attached stem growth, because these terminal shoot deaths occurred so frequently that they could be considered part of regular development. With *Betula*, the number of dead structural branch tips was counted as the number of junctions between long shoots or converted short shoots, plus one, because *Betula* branches usually produced only short shoots before dying. Dead inflorescences of *Ledum* or *Betula* were not counted, because inflorescences are always determinate. Dead inflorescences older than about five years could not always be distinguished from dead vegetative branches in *Ledum*. However, the number of dead branches whose origin was uncertain was very small and did not affect the conclusions.

Aboveground biomass harvests

To estimate abundance in the community, at the time of peak biomass (late July) in 1996 we harvested all aboveground biomass of each of the three species previously analyzed for individual growth from five randomly selected 20 × 20 cm quadrats within each plot (a total of 20 quadrats per treatment), according to the method of Shaver and Chapin (1991). Quadrats were chosen randomly along a line transect in previously undisturbed portions of the plots.

Within each quadrat, we counted the number of currently active vegetative meristems (''growing points'') and inflorescences for each species, and the numbers of currently active short and long shoots for *Betula*. We separated biomass into current year's production of leaves and shoots, current year's inflorescences, old live stems, old live leaves (*Ledum* only), and dead stems. Material was dried at 65°C for 48 h and weighed. Values were averaged among the five quadrats within each plot, then among the four blocks, and are presented as the means (± 1 SE) among blocks ($n = 4$) for each treatment.

Because the distribution of *Salix* is very patchy, we encountered *Salix* too rarely in quadrat harvests to permit statistical analysis of its abundance from these data. To get another estimate of *Salix* abundance in the community, in late July 1997 we counted the total number of ramets in the undisturbed half (2.5 × 2.5 m) of each of the greenhouse plots and in a randomly located area of the same size in each of the control and fertilized plots. For this purpose, a ramet was defined as a live stem entering the moss layer or ground surface, or two or more stems joined < 2.5 cm under the surface. These ramets were of different ages and sizes, and some were probably connected farther underground.

Photosynthesis

To determine whether experimentally induced changes in net photosynthesis rate could help explain experimentally induced differences in biomass, in late July 1995 we measured net photosynthetic gas exchange at saturating light intensity on two replicate shoots from each of the three species in each plot. Leaves of deciduous species were fully developed, while *Ledum* shoots included both mature leaves (formed in the previous year) and new leaves that were still expanding. Because new *Ledum* leaves do not finish expanding until after deciduous leaves senesce, we could not measure gas exchange on fully mature leaves of all species at the same time. Deciduous species showed no signs of senescence when our measurements were made. Net photosynthesis was measured in the field under partly cloudy conditions on attached shoots using a 0.25-L leaf chamber attached to a portable photosynthesis system (LiCor 6200; LI-COR, Lincoln, Nebraska). The chamber was fitted with a light source (Q-beam; Quantum Devices, Madison, Wisconsin) that delivered constant saturating intensity (2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of cool red light. Shoots were exposed to this light for three minutes at ambient CO_2 concentration prior to making three replicate gas exchange measurements per shoot. Temperature in the chamber did not increase by more than 0.5°C during measurement. Following measurement, the shoot was cut from the plant and trimmed so that only that portion of leaves and stems inside the seals of the chamber was left. Leaves were detached and their area was measured using a leaf-area meter (LI 3000A, LI-COR). Leaves and stems were dried at 65°C for 48 hours and weighed. Because leaves of these species are so small, it was not possible to measure the net photosynthesis of leaves without including attached stems. Accordingly, our estimates of saturating net photosynthesis underestimate the true net photosynthetic rate by the respiratory activity of the stem within the chamber.

Canopy characteristics and Ledum *leaf morphology*

To document experimentally induced changes in canopy structure and amount of light reaching the understory, we measured intensity of photosynthetically active radiation at the top of the canopy, and at the ground or moss surface below, in the center of every other 20 × 20 cm quadrat within a 1 × 1 m grid in each experimental plot. Light measurements were made at midday under clear skies in mid-August 1997 with a quantum sensor and light meter (LI 250; LI-COR). Canopy height and identity of species at the top of the canopy were recorded at each location where light measurements were made. Leaf area index (LAI) was measured at the same location with a plant canopy analyzer (LAI 2000, LI-COR) a few days later under cloudy sky conditions.

To determine whether *Ledum* was showing acclimation to shading created by canopy development in the experimental plots, three nondestructive measurements of leaf morphology were made on four randomly selected *Ledum* ramets from the understory in each plot in August 1997. For each ramet, we measured length and width of the three widest leaves and determined whether leaf margins were rolled, partially rolled, or flat (unrolled).

Statistical analyses

Because of the large stimulation of growth by the fertilizer plus greenhouse treatment, most data did not meet assumptions of homogeneity of variance and normality. Data were transformed using the algorithms $y = \log(x + 1)$ or $y = 2 \arcsin(\sqrt{x})$, after which variance was sufficiently homogeneous (Cochran's test; Winer et al. 1991) and the data were sufficiently normally distributed (Lilliefors test; SYSTAT 1992) to permit analysis of variance. Data for each species were analyzed as a two-way ANOVA, with fertilization, greenhouse treatment, and block as main effects, and with a greenhouse × fertilizer interaction effect. Categorical data for *Ledum* leaf margins were analyzed with contingency tables, and differences were tested with a maximum likelihood ratio test (Sall and Lehman 1996). This analysis showed significant differences ($P < 0.001$) in 3 × 4 contingency tables. To determine significance of main effects for *Ledum* leaf margins, 2 × 2 contingency tables were constructed comparing both fertilized treatments with unfertilized treatments, and both greenhouse treatments with treatments that lacked greenhouses. Standard errors are presented for measured parameters except for some measurements for *Salix* obtained from the quadrat harvests, where only a single nonzero value was obtained; then, no error bars are shown.

RESULTS

Environmental effects of the treatments

Detailed descriptions of the environmental effects of treatments identical to ours have already been published (Chapin et al. 1995, Shaver et al. 1998). Because our results agree well with those previously published, we present them only briefly here. All eight years of microclimate data pertaining to the present experiment are available electronically on the Arctic LTER web site[4].

The major effect of the greenhouses was to increase average daily air temperature by 3.7°C (Table 1). Average daytime maximum air temperatures increased substantially, while nocturnal minimum temperatures did not change much during the time that the greenhouse plastic was in place (Table 1). The cumulative effect was that degree-day accumulations (sums of mean daily temperatures > 0°C) increased by 28–43%

[4] URL: ⟨http://sgi.mbl.edu/html/ECOSYSTEMS/lterhtml/arc.html.⟩

TABLE 1. Average daily mean, average daily minimum, and average daily maximum, air temperatures for each summer month and sums of degree-days over 0°C for the whole growing season in greenhouse treatment and control plots.

Year and month	Air temperature (°C)					
	Control			Greenhouse		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
1993						
May†		2.9				
June	5.7	9.0	14.4	4.6	13.6	30.8
July	8.3	13.7	18.5	8.3	20.0	33.3
August	2.5	6.0	9.4	0.8	8.7	14.2
September	−4.7	−0.9	2.7			
Degree-day sums		1063			1479	
1994						
May	−5.1	0.3	5.1			
June	1.5	6.8	11.5	2.2	13.7	25.8
July	8.0	13.6	18.6	7.7	19.6	32.6
August	4.5	9.1	13.5	6.6	11.1	25.1
September	−6.5	−2.9	0.6			
Degree-day sums		1033			1481	
1995						
May	−2.5	2.2	7.7			
June	3.0	7.6	12.3	3.4	10.8	19.8
July	6.7	11.1	15.3	6.7	15.2	25.0
August	1.8	6.5	11.0	1.1	8.8	17.6
September	−0.5	3.6	7.7	−0.5	3.3	7.1
Degree-day sums		1026			1312	

Notes: Greenhouses were in place from June through August. Temperature values for May and September in control plots were used in the calculation of degree-day sums for both greenhouse treatment and control plots, because temperatures over the entire period may affect growth. Degree-day sums were calculated as the sums of daily mean temperatures of all days with mean temperature greater than 0°C; they cannot be inferred directly from the monthly mean temperatures because the calculation excludes days with mean temperature <0°C that contribute to the monthly means.

† Estimated from data collected at Imnavait Creek; no maximum and minimum temperatures available.

in the greenhouses during June, July, and August (Table 1).

Greenhouses did not significantly increase soil temperature at any of the depths we measured, but replicate measurements varied considerably. However, greenhouses significantly increased depth of thaw, which is an integrated measure of soil temperature, in both years that we measured it (Table 2). Fertilization significantly decreased thaw depth in 1993, but not in 1997 (Table 2), probably indirectly by increasing canopy development and resultant shading of the ground surface.

The major undesired effect of the greenhouse treatment was to decrease PAR by ~20%, as shown previously (Chapin et al. 1995). However, previous shading experiments showed that biomass and production are not very sensitive to long-term reductions in light input of 50% or more; shading decreased production only 20% after nine years (Chapin et al. 1995, Shaver et al. 1998, Jonasson et al. 1999). Simulation analyses (McKane et al. 1997) also indicate that reduced light intensity in combination with greenhouse warming would lead to no change in carbon stocks over the long term, compared to a very slight increase in carbon stocks if light were not reduced.

Greenhouses also reduced average relative humidity by up to 24%. The largest decrease occurred early in the season when radiation inputs were highest. This decrease would be expected because air temperature increased with little change in absolute humidity. Plants generally respond to short-term decreases in atmospheric humidity with decreased stomatal conductance (Schulze and Hall 1982, Grantz 1990). However, over longer periods acclimation occurs, and effects of other parameters, such as prevailing light, are likely to be more significant than humidity (Grantz 1990). Thus, the primary effect of the greenhouses was to increase air temperature, as intended. We do not claim that they have no other effects, nor that they closely simulate future climate under global warming.

Biomass, growing points, inflorescences

Fertilization significantly increased the stem biomass of 15-yr-old ramets from all three species (Fig. 1a, Table 3). Greenhouse treatment, on the other hand, significantly increased the stem biomass of ramets of *Bet-*

TABLE 2. (A) Depth of soil thaw in late summer and (B) ANOVA for treatment effects.

A) Mean thaw depth (cm)

Date	Treatment			
	C	F	GH	GHF
20 Aug 1993	47.1 (1.7)	43.2 (0.7)	52.8 (1.3)	51.4 (1.7)
6 Aug 1997	48.8 (1.8)	45.2 (1.3)	61.0 (3.0)	61.0 (3.0)

B) ANOVA

Date	Source	*F*	df	*P*
20 Aug 1993	Block	1.13	3, 122	NS
	F	5.85	1, 122	*
	GH	38.72	1, 122	***
	F × GH	1.22	1, 122	NS
6 Aug 1997	Block	9.20	3, 153	***
	F	2.27	1, 153	NS
	GH	135.68	1, 153	***
	F × GH	2.27	1, 153	NS

Notes: A thin metal probe was pushed into the ground, and depth of the active layer (from the moss surface to the bottom of the thawed soil) was recorded at 8–10 locations per plot. Mean values are reported in panel (A), with 1 SE in parentheses (n = 4 blocks). Panel (B) reports results from a two-way ANOVA for thaw depth at each date. Data were not transformed. Abbreviations: C, control; F, fertilizer treatment; GH, greenhouse treatment; GHF, fertilizer plus greenhouse treatment.

*$P \leq 0.05$; ***$P \leq 0.001$; NS = not significant.

ula, but not of the other species (Table 3). There was no significant fertilizer × greenhouse interaction for any species using log-transformed data, presumably because the interactions were not greater than the product of the individual treatment effects. The increase in *Betula* ramet biomass in the greenhouse plus fertilization treatment was more than additive, but less than multiplicative, relative to greenhouse treatment and fertilization separately.

The relative increase in stem biomass caused by fertilizer plus greenhouse treatment was greater for *Betula* ramets (approximately sixfold) than for either *Salix* or *Ledum* ramets (two- to threefold) (Fig. 1a). This may help explain why, at the community level, stem biomass per unit area showed a significantly positive response to fertilization only for *Betula* (Fig. 1b, Table 3). *Ledum* stem biomass per unit area was significantly depressed by fertilization, while greenhouse treatment increased *Ledum* stem biomass per unit area slightly (Fig. 1b, Table 3). *Salix* occurred too sparsely in the community for statistical analysis on its stem biomass per unit area to be carried out from these measurements. However, *Salix* abundance in the community was clearly depressed by fertilization and to a lesser extent by greenhouse treatment (Fig. 2), as measured by the total number of ramets in a larger area (2.5 × 2.5 m) than that of the quadrat (20 × 20 cm) used to determine biomass per unit area for the other species.

Treatment effects on the number of current year's growing points (i.e., active meristems) per ramet were similar to those described for stem biomass (Fig. 3a, Table 3). Again, fertilization stimulated all three species to increase the number of growing points in 15-yr-old ramets, although the increase for *Salix* was only marginally significant (P = 0.066). Greenhouse treatment without fertilization tended to increase the number of growing points per *Betula* ramet (P = 0.061), but had no significant effect on the number of growing points of other species. The relative increase in growing points with greenhouse plus fertilizer treatment was much larger for *Betula* (between four- and fivefold) than for the other species (1.2 to threefold). At the community level, fertilization significantly increased the growing points of *Betula* per unit area, while significantly decreasing growing points of *Ledum* (Fig. 3b, Table 3).

In *Betula*, fertilization alone stimulated production of inflorescences in individual ramets, and also per unit area in the community (Fig. 4). This increase was

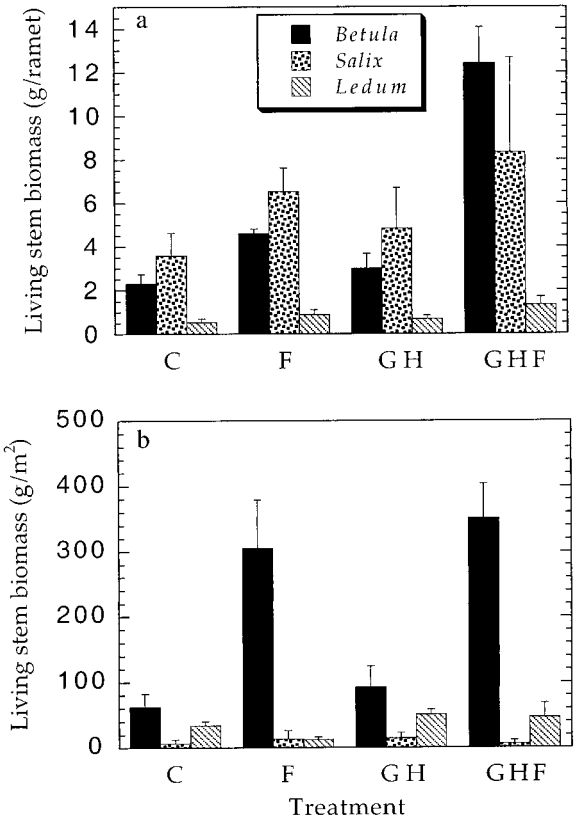

FIG. 1. Live stem biomass of *Betula*, *Salix*, and *Ledum* (a) per 15-yr-old ramet measured in 1995 and (b) per square meter from quadrat harvests of aboveground biomass in the community, measured in late July 1996. The data do not include primary stem biomass generated in the year of harvest. Treatments: C, control (no manipulation); F, fertilized with 10 g/m² N and 5 g/m² P (see *Methods*); GH, temperature elevated with plastic greenhouses; GHF, temperature elevated with greenhouses plus fertilizer (same fertilizer amounts as the F treatment). Error bars indicate + 1 SE (n = 4 blocks).

TABLE 3. Results of two-way ANOVAs on major variables for each species.

	Source of variation											
	Block			F			GH			F × GH		
Variable	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Individual ramets												
Live stem biomass												
Betula	0.10	3, 40	NS	28.68	1, 40	***	8.44	1, 40	**	2.43	1, 40	NS
Salix	1.36	3, 32	NS	2.96	1, 32	†	0.18	1, 32	NS	0.44	1, 32	NS
Ledum	0.45	3, 41	NS	3.79	1, 41	*	1.98	1, 41	NS	0.05	1, 41	NS
Current growing points												
Betula	0.30	3, 40	NS	34.54	1, 40	***	3.73	1, 40	†	1.41	1, 40	NS
Salix	2.10	3, 32	NS	3.22	1, 32	†	0.66	1, 32	NS	0.09	1, 32	NS
Ledum	0.56	3, 41	NS	11.56	1, 41	**	0.47	1, 41	NS	0.24	1, 41	NS
(Long shoots)/(total vegetative shoots)												
Betula‡	3.44	3, 40	*	87.24	1, 40	***	0.01	1, 40	NS	2.06	1, 40	NS
Maximum age of short shoots												
Betula§	0.53	3, 40	NS	44.57	1, 40	***	2.43	1, 40	NS	0.00	1, 40	NS
(Short shoot stem biomass)/(total stem biomass)												
Betula§	2.03	3, 40	NS	44.62	1, 40	***	3.18	1, 40	†	2.54	1, 40	NS
Dead structural branches												
Betula	2.13	3, 40	NS	3.85	1, 40	†	1.60	1, 40	NS	4.77	1, 40	*
Salix	0.06	3, 32	NS	2.15	1, 32	NS	0.12	1, 32	NS	2.21	1, 32	NS
Ledum	1.77	3, 41	NS	13.66	1, 41	***	3.84	1, 41	†	0.28	1, 41	NS
Ledum leaf morphology												
Leaf length§	3.94	3, 185	**	16.27	1, 185	***	31.70	1, 185	***	0.07	1, 185	NS
Leaf width§	4.26	3, 185	**	353.40	1, 185	***	23.78	1, 185	***	1.05	1, 185	NS
Rolling of leaf margin‖						***			NS			
Quadrat harvests												
Live stem biomass												
Betula	1.36	3, 73	NS	59.10	1, 73	***	2.23	1, 73	NS	0.01	1, 73	NS
Ledum	2.01	3, 73	NS	8.44	1, 73	**	4.82	1, 73	*	0.39	1, 73	NS
Current growing points												
Betula	1.79	3, 73	NS	51.79	1, 73	***	1.51	1, 73	NS	2.77	1, 73	NS
Ledum	2.50	3, 73	†	19.48	1, 73	***	1.78	1, 73	NS	2.69	1, 73	NS
(Long shoots)/(total vegetative shoots)												
Betula	3.03	3, 70	*	25.61	1, 70	***	1.64	1, 70	NS	0.01	1, 70	NS
Dead stem biomass												
Betula	1.106	3, 73	NS	8.30	1, 73	**	1.15	1, 73	NS	2.09	1, 73	NS
Ledum	0.83	3, 73	NS	0.65	1, 73	NS	1.28	1, 73	NS	3.29	1, 73	†

Notes: Data were log-transformed to achieve homogeneity of variance unless otherwise noted. *Salix* was so patchy in the community that, for quadrat harvests, the assumptions of analysis of variance could not be met. For sources of variation, block = main effect of block treatment, F = main effect of fertilizer treatment, GH = main effect of greenhouse treatment, F × GH = fertilizer-by-greenhouse interaction term in the ANOVA.

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; †$P \leq 0.1$; NS, not significant ($P > 0.1$).

‡ Data were transformed using the formula $y = 2 \arcsin(\sqrt{x})$.

§ Data were not transformed.

‖ Categorical data on *Ledum* leaf margins were compared using contingency tables, and differences were tested with a likelihood-ratio test (see *Methods*). It was not possible to test for an interaction effect.

caused both by an increase in the number of inflorescences per flowering ramet, and by an increase in the frequency of ramets that flowered (Fig. 5a,b). Flowering of *Betula* was not promoted by the fertilizer plus greenhouse treatment.

Photosynthesis

Fertilization did not increase the light-saturated net photosynthetic rate per unit of *Betula* leaf area (Fig. 6). Fertilization actually decreased the unit area net photosynthetic rate for *Betula* and *Ledum*, but the decrease was not significant. Greenhouse treatment significantly ($P = 0.005$) increased net photosynthesis for all species (Fig. 6), probably because it was measured at a higher temperature in the greenhouses (18°C) than in the other treatments (16°C). However, in three-way analysis of variance, there were no significant differences among species in net photosynthetic rate in any treatment, and no significant species × greenhouse or species × fertilizer interactions. Fertilization decreased, or did not significantly increase, net photosynthesis of tussock tundra species in several

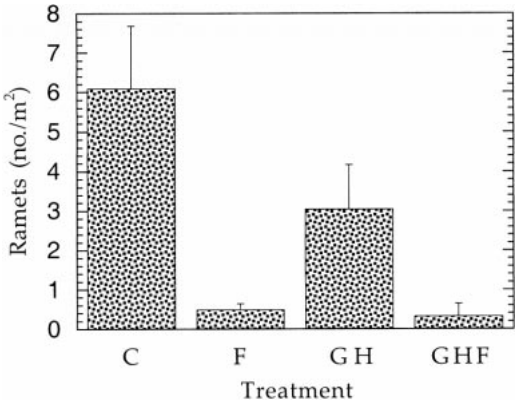

FIG. 2. *Salix* abundance. The total number of live stems entering the moss mat were counted in undisturbed 2.5 × 2.5-m subplots. Stems connected < 2.5 cm under the moss surface were counted as one ramet. Treatment abbreviations are as in Fig. 1. Error bars indicate + 1 SE.

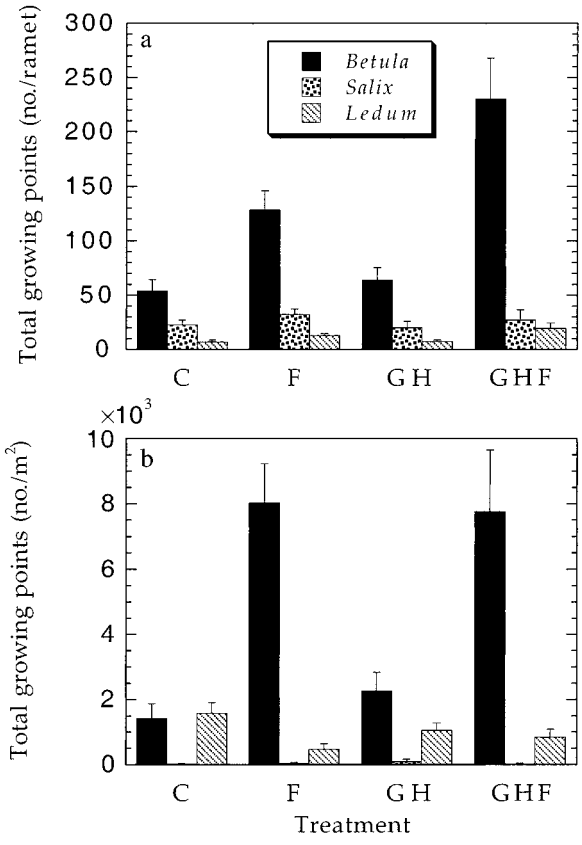

FIG. 3. Total numbers of growing points (shoots growing from active meristems in the current year) for *Betula*, *Salix*, and *Ledum*: (a) per 15-yr-old ramet measured in 1995, (b) per square meter from quadrat harvests of aboveground biomass, measured in late July 1996. Total growing points include inflorescences and both short and long vegetative shoots of *Betula*. Treatment abbreviations and species legend are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

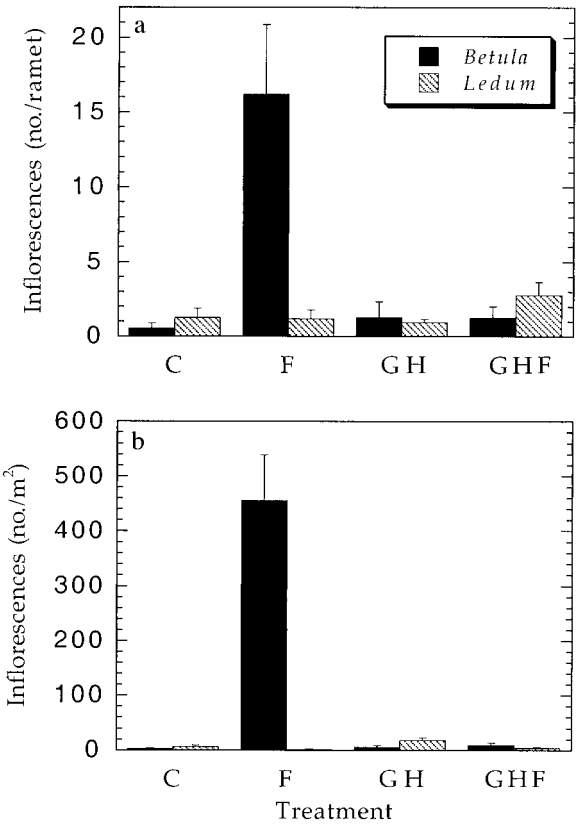

FIG. 4. Total number of inflorescences for *Betula* and *Ledum*: (a) per 15-yr-old ramet, over the period 1993–1996, (b) per square meter from quadrat harvests of aboveground biomass, 1996. *Betula* inflorescences detected were mostly female, because male inflorescences do not persist well late in the season. *Salix* inflorescences of either sex are not persistent unless females are fertilized and could not be reliably detected with our methods. Treatment abbreviations and species legend are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

studies (Bigger and Oechel 1982, Matthes-Sears et al. 1988, Oberbauer et al. 1989), but in one an increase in gross photosynthesis was seen (Chapin and Shaver 1996). Although net photosynthetic rate did not differ among species in this study, the total photosynthetic carbon gain for fertilized *Betula* plants was undoubtedly larger than for the other species, because of its greater growth (Fig. 1), greater numbers of growing points (Fig. 3), and greater leaf area (Chapin and Shaver 1996). This led us to consider whether changes in allocation and growth might be important in explaining the different responses of the species to the treatments.

Branch allocation

Betula shoot growth involves both short and long shoots. Long shoots undergo extensive elongation and produce 6–12 leaves. Short shoots elongate < 2 mm per year and produce only 1–3 leaves. Only long shoots have potential for additional branch production, be-

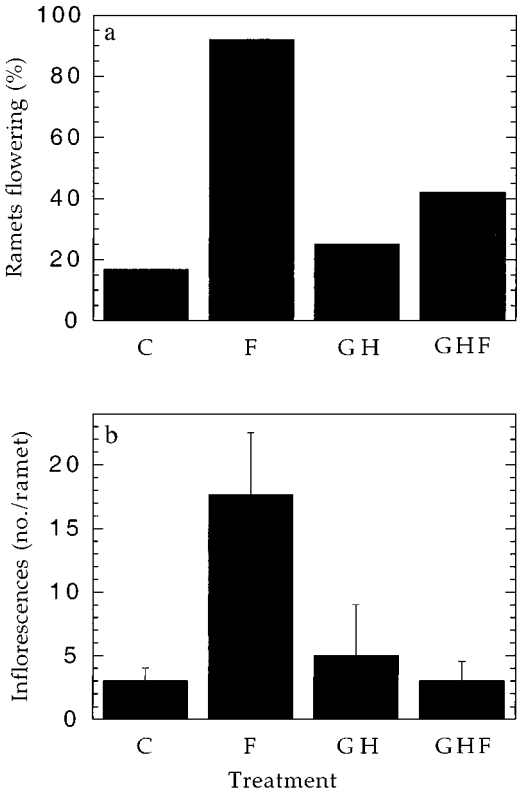

FIG. 5. Flowering frequency and inflorescence abundance in *Betula* ramets: (a) flowering frequency (percentage of ramets with any inflorescences visible), (b) number of inflorescences per ramet among those ramets with at least one inflorescence visible. Treatment abbreviations and species legend are as in Fig. 1. Error bars in (b) indicate + 1 SE (n = 4 blocks).

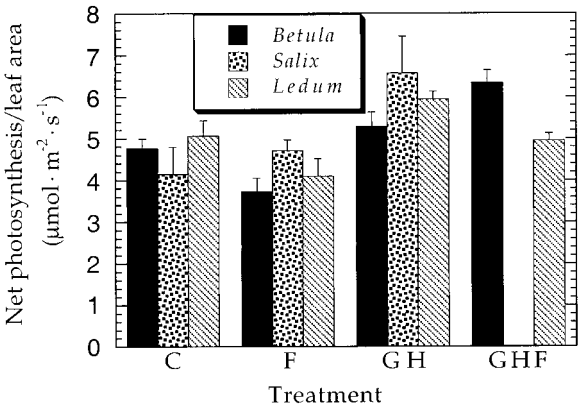

FIG. 6. Net photosynthesis per unit leaf area at saturating light intensity (2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$), measured in late July 1995, for shoot tips of *Betula*, *Salix*, and *Ledum*. No *Salix* shoot tips were measured in the GHF treatment, because all ramets had previously been harvested for growth analysis. Treatment abbreviations are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

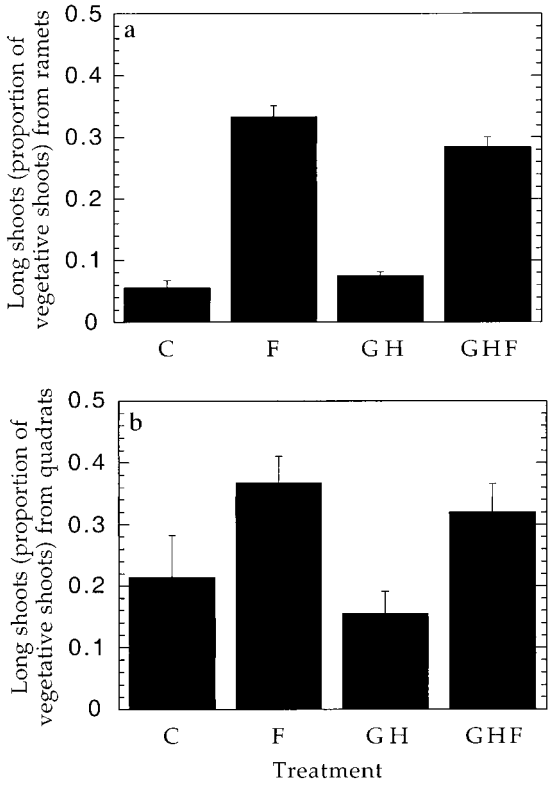

FIG. 7. The proportion of total vegetative shoots that are long shoots in *Betula*: (a) per 15-yr-old-ramet, measured in 1995, (b) in the community, from quadrat harvests in 1996. Treatment abbreviations are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

cause they produce viable buds in the axils of their leaves, whereas short shoots do not. Fertilization dramatically altered the relative abundance of short and long shoots. Control ramets of *Betula* produced mainly short shoots; only 5–6% of their current year's growing points were long shoots (Fig. 7a). Fertilization significantly increased the proportion of long shoots, to 30% (Fig. 7a, Table 3). In the quadrat samples, fertilization had a similar, significant effect on the proportion of long shoots in the community (Fig. 7b, Table 3).

This change in branch allocation with fertilization caused a large difference in the number of structural branches in *Betula* ramets from different treatments to develop over time. After seven years of treatment, there was a 9–16 fold difference between ramets from the two fertilizer treatments and control ramets in the number of current year's growing points that were long shoots (Figs. 3a, 7a). This large difference occurred because enhanced production of long shoots from axillary buds year by year caused an multiplicative increase in the total number of structural branches with time.

Salix and *Ledum* do not have short/long shoot di-

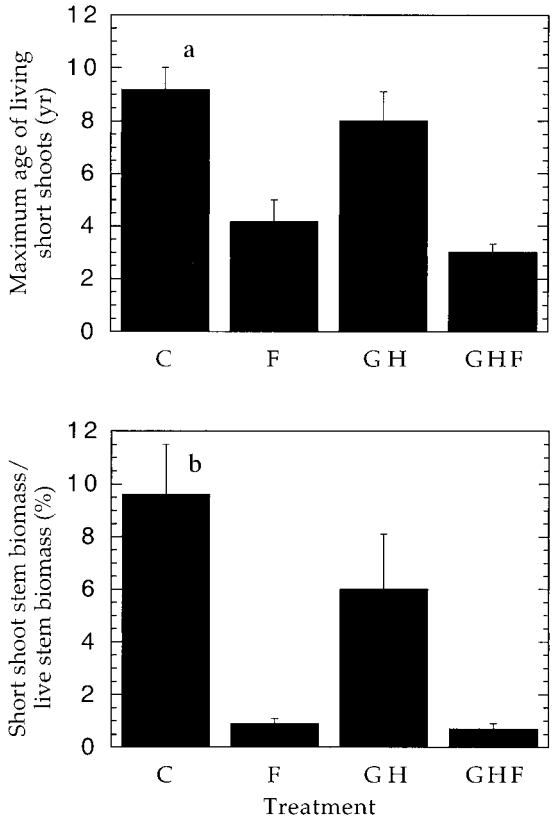

FIG. 8. (a) Maximum age of living short shoots (mean among ramets of each treatment), per 15-yr-old ramet of *Betula*. (b) Biomass of stems of living short shoots divided by total live stem biomass, per 15-yr-old ramet of *Betula*. Biomass data do not include primary stem biomass formed in the current year. Treatment abbreviations are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

morphism. Though fertilization slightly increased the number of current year's growing points in *Salix* ramets (Fig. 3a), there was no difference between ramets from control and fertilized plots in the numbers of branches in any age class older than the current year. Although fertilization increased the number of *Ledum* branches 2–3 fold, this increase was much smaller than for *Betula* ramets (Fig. 3a).

In addition to investing more heavily in long shoots, fertilized *Betula* ramets also stopped maintaining their existing short shoots. The average maximum age of living short shoots on 15-yr-old ramets declined from 9 yr to 3–4 yr with fertilization, as older short shoots died (Fig. 8a, Table 3). In addition, the percentage of stem biomass represented by short shoots of all ages dropped from $\sim$ 10% in the control ramets to $<$ 1% in ramets from the fertilizer treatments (Fig. 8b).

The change in the proportion of *Betula* branches that were long shoots could have occurred either by converting existing short shoots into long shoots or by changing the fates of newly formed buds on the current year's long shoots. Fertilization had no significant effect on the frequency of conversions of short shoots into long shoots, and roughly half of the conversions detected occurred prior to the treatments (data not shown). The shift toward production of long shoots in fertilized *Betula* ramets must have resulted mainly from changing the fates of the buds that were formed in axils of long shoot leaves during the experiment.

Mortality

Species abundance is determined by both growth and mortality. We measured numbers of attached dead branches in ramets and dead stem mass in quadrat harvests as indicators of branch mortality within individual ramets and in the community (Fig. 9). The combination of fertilizer and greenhouse treatment significantly increased the number of attached dead branches in ramets of *Betula*, but there was no significant effect of either greenhouse treatment or fertilization alone

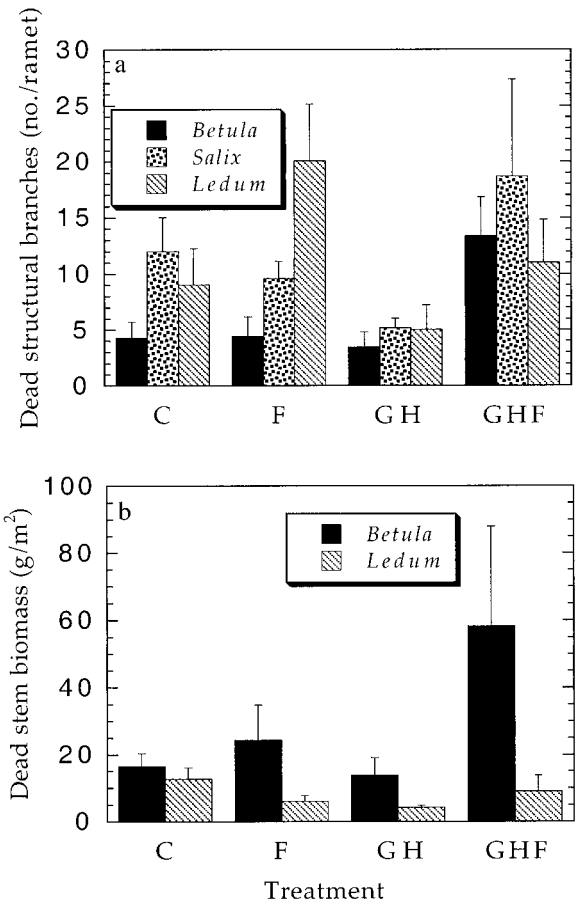

FIG. 9. Estimates of mortality within ramets and in the community: (a) total number of dead structural branches per ramet, for *Betula*, *Salix*, and *Ledum*, (b) dead stem biomass from quadrat harvests, for *Betula* and *Ledum*. So few of the quadrat samples contained any dead stem biomass of *Salix* that those data are not presented. Treatment abbreviations and species legend are as in Fig. 1. Error bars indicate + 1 SE (n = 4 blocks).

TABLE 4. Light intensity, mean canopy height, leaf area index (LAI), and mean canopy composition.

Variable	Treatment			
	C	F	GH	GHF
Incident light intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1050 ± 66	1064 ± 109	815 ± 95	776 ± 22
Understory light intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	686 ± 70	81 ± 25	382 ± 145	85 ± 14
Canopy height (cm)	16 ± 2	36 ± 2	29 ± 8	65 ± 8
Leaf area index	1.1 ± 0.1	3.2 ± 0.1	2.3 ± 0.1	3.1 ± 0.1
Relative abundance at the top of canopy (%)				
Eriophorum vaginatum	35.1 ± 9.8	6.9 ± 4.7	41.8 ± 11.4	0 ± 0
Betula nana	26.7 ± 9.4	91.3 ± 4.2	44.4 ± 11.9	93.2 ± 4.7
Salix pulchra	14.5 ± 9.7	0 ± 0	5.3 ± 1.8	5.0 ± 5.0
Rubus chamaemorus	8.6 ± 2.0	1.8 ± 1.8	0 ± 0	0 ± 0
Cassiope tetragona	6.8 ± 3.2	0 ± 0	1.6 ± 1.6	0 ± 0
Ledum palustre	5.6 ± 2.2	0 ± 0	7.0 ± 2.6	1.8 ± 1.8
Vaccinium uliginosum	1.3 ± 1.3	0 ± 0	0 ± 0	0 ± 0
Carex bigelowii	1.3 ± 1.3	0 ± 0	0 ± 0	0 ± 0

Notes: Light intensity was measured above the canopy and at ground surface or the top of the moss layer in the center of every other 20 × 20-cm quadrat in a 1-m^2 grid. Species identity at the top of the canopy was determined at each location where light measurements were made. LAI was measured using a plant canopy analyzer in the same location. Data are means ± 1 SE; $n = 4$ blocks. Treatment abbreviations are as in Table 2.

(Fig. 9a, Table 3). A qualitatively similar pattern was seen in *Salix* ramets, but differences were not statistically significant (Fig. 9a, Table 3). Fertilization significantly increased the number of attached dead branches in *Ledum* ramets (Fig. 9a, Table 3). Many of these attached dead branches in *Ledum* ramets were very small, with negligible mass.

In quadrat harvests, dead stem mass of *Betula* was significantly increased by fertilization (Fig. 9b, Table 3). Dead stem mass was highly variable for *Ledum;* neither greenhouse treatment nor fertilization had a significant effect (Fig. 9b, Table 3). No data for *Salix* are presented, because virtually no dead stem biomass of *Salix* was encountered in the quadrat harvests. For *Betula,* comparison of ramet and quadrat harvests suggests that increase in dead stem mass in the fertilization treatment was caused primarily by mortality of shoots attached to branch segments older than 15 yr, which were not sampled in the ramet harvests. However, the fertilization plus greenhouse treatment showed a significant increase in branch mortality within 15-yr-old ramets of *Betula* (Fig. 9a), which may partially account for the increase in dead stem mass of *Betula* in this treatment (Fig. 9b).

Neither attached dead branch number nor dead stem mass are perfect indicators of mortality, because dead material that decomposed or was removed from the plot would not be recorded. Nonetheless, these data suggest that fertilization increased stem mortality of *Betula* and of at least the smaller shoots in ramets of *Ledum.*

Canopy characteristics

Betula's extensive branching under fertilization caused the structure and height of the canopy to change substantially. The LAI of the vegetation nearly tripled in the two fertilization treatments, while doubling under greenhouse treatment alone (Table 4). Canopy height increased 2–4 fold in the two fertilization treatments, and 1.8-fold under greenhouse treatment alone (Table 4). Increased canopy height in the greenhouse treatment, although no incease in biomass was seen, may have influenced the photometric measurement of LAI. At the same time, species richness at the top of the canopy decreased from eight species in the control (of which *Betula* was the second most common) to five species in the greenhouse-only treatment and three species in the two fertilizer treatments (Table 4). In the two fertilizer treatments, *Betula* was the top of the canopy in > 90% of the measurements (Table 4). As a consequence of this canopy development, light inten-

TABLE 5. Leaf morphology in ramets of *Ledum.*

Variable	Treatment			
	C	F	GH	GHF
Leaf length (mm)	11.8 ± 0.9	14 ± 1	4 ± 1	16.4 ± 0.7
Leaf width (mm)	2.1 ± 0.1	4.7 ± 0.3	2.9 ± 0.5	5.2 ± 0.1
Leaf margin†				
Rolled margins	15	0	9	0
Partially rolled/flat	1	4	5	0
Flat margins	0	12	2	16

Notes: Data are means ± 1 SE; $n = 4$ blocks. Categorical data for ramets with different leaf margin characteristics were pooled for each treatment. Treatment abbreviations are as in Table 2.

† Number of ramets with two-thirds or more of sampled leaves in each category.

sity in the understory as a fraction of incident intensity was reduced, in the fertilizer treatments, to as little as 12% of the control value (Table 4).

Although *Ledum* was a significant part of the canopy in control plots, it became virtually confined to the understory in the fertilizer treatments. We wondered if it showed signs of acclimation to shading. *Ledum* leaves were significantly longer and more than twice as wide in the two fertilizer treatments as in the control treatment (Tables 3 and 5). The width increase was caused largely by unrolling of the leaves (Tables 3 and 5). *Ledum* ramets in the greenhouse-only treatment had leaf morphology intermediate between that of control and fertilized *Ledum* ramets (Table 5), which is consistent with the intermediate level of canopy development in that treatment (Table 4).

Shoot density per unit area

Our data indicate that the abundance of *Ledum* and *Salix* in the community can decline even while growth of their individual ramets is stimulated by an environmental change. This is true even though changes in growth of individual plants largely determine the response of community-level biomass in this ecosystem, because recruitment of new individuals is very rare (McGraw and Shaver 1982, McGraw and Fetcher 1992). Differences between ramet growth and species abundance must be caused by changes in the density of shoots per unit area.

Shoot density per unit area increased for *Betula* in all treatments, because the response of live stem biomass was always larger in the quadrat harvests than in the ramets (Fig. 1). Increases in *Betula* shoot density in the two fertilizer treatments were caused by increased production, not by decreased mortality, because fertilization significantly increased dead stem mass in the quadrat harvests (Fig. 9b). However, comparing ratios of fertilizer-treated to control ramets with the same ratios for quadrat harvests, only 40% of the increase in stem biomass (Fig. 1) and in growing points (Fig. 3) in the fertilizer-only treatment appears to have come from stem segments that were 15 yr old or younger when we made our measurements. The increase in *Betula* shoot density apparently resulted from growth of buds on stems older than 15 yr; we did not see any *Betula* seedlings. Potential activity of basal buds for many years following formation is a genetic characteristic of *Betula nana* (Valanne and Sulkinoja 1991).

It is not clear whether declines in shoot density of *Salix* and *Ledum* in fertilized plots (Figs. 1, 2) occurred because of increased shoot mortality or decreased production of shoots from older stems. Increased shoot mortality contributed to the decline in shoot density in *Ledum,* because fertilized ramets of *Ledum* had significantly more attached dead branches than ramets from other treatments (Fig. 9a). However, dead stem biomass was actually lower in fertilized than in control plots (Fig. 9b), and thus could not account quantitatively for the decline in live *Ledum* stem biomass in the community with fertilization. This suggests that reduced production of shoots from older stems was also important.

Discussion

Mechanism of change in community composition

The results of our quadrat harvests are consistent with those of previous experiments on tussock tundra, in which fertilization produced large increases in vascular plant biomass and production and a decline in plant diversity (Chapin et al. 1995). Such declines in diversity have been seen in other ecosystem fertilization experiments (Silvertown 1980, Huenneke et al. 1990). Our results reveal an important mechanism that underlies the fertilization-induced change in composition in the tundra community. This mechanism is the superior developmental plasticity of one species in recruiting additional apical meristems to participate in shoot elongation.

In this ecosystem, the increase in productivity and vascular plant biomass with increased nutrient availability was caused almost entirely by the growth of *Betula nana,* while other shrub, graminoid, and herbaceous species declined in abundance (Chapin et al. 1995). According to elementary plant growth analysis (Evans 1972, Hunt 1978), an increase in relative growth rate requires an increase either in photosynthetic rate per unit leaf area (NAR) or in leaf area per unit of total plant biomass (LAR). However, fertilization caused no significant differences between *Betula* and the other species in NAR (Fig. 6). The increased growth of *Betula* relative to the other species thus implies an increase in its LAR. Our data indicate that this occurs because under fertilization the number of *Betula's* leaf-producing long shoots increases multiplicatively each year. After several years, this leads to a dense *Betula* canopy and the biomass of other species declines. *Betula* shows superior, advantageous, developmental plasticity in response to fertilization.

Betula's large growth response to fertilization and subsequent dominance in the community result from its ability to greatly increase its number of structural branches. Greater branching is possible because *Betula* has a large pool of active meristems, in the form of existing short shoots and axillary buds on long shoots that grow as either short or long shoots in the year after their formation. In addition, *Betula* can alter the fate of preexisting shoots from short to long and vice versa. Under unfertilized conditions, most axillary buds grow as short shoots. Short shoots produce so little wood and so few leaves that carbon costs (for wood and secondary metabolites) and nitrogen costs (for photosynthetic machinery) must be appreciably less than for long shoots. This is probably why dedication of most buds to short shoots under unfertilized, nutrient-limited conditions is advantageous, even though photosyn-

thetic return from short shoots is less than from long shoots, because short shoots produce fewer leaves than long shoots do. However, short shoots cannot increase the number of actively growing shoots on the plant, as long shoots do by producing axillary buds. Under fertilized conditions, *Betula* greatly increases the proportion of apical meristems that grow as long shoots. Long shoots produce 2–3 times as much leaf area as short shoots do, increasing the shrub's total photosynthetic return in proportion, and permitting dense canopy development.

Both *Ledum* and *Salix* appear to have less developmental plasticity in meristem activity than does *Betula,* and may be limited in their ability to respond to fertilization by increasing the number of active meristems. *Ledum* does not usually produce lateral branches unless the apical growing point dies, because of either flowering or vegetative mortality. Although *Salix* produces buds in the axils of all current year's leaves, normally no more than two or three of these grow the following year. Some that do grow become inflorescences, leaving only one or two vegetative shoots. Lower buds normally do not grow, although they will if the upper part of the shoot dies, which suggests strong apical dominance. This pattern is maintained under fertilization, even though branches in *Salix* ramets from the fertilized treatments are much longer and heavier (Fig. 1a). Because both *Ledum* and *Salix* make only long shoots, their respiratory and resource costs per active meristem must be higher than for *Betula.* This may have selected against their maintaining as many active meristems as *Betula* does.

Developmental plasticity, growth rate, and meristem availability

Among many plant species, there appears to be a trade-off between attributes that confer the ability to acquire resources and grow quickly in productive habitats, and those attributes, such as investments in secondary metabolites and long-lived leaves, that permit retention of resources in unproductive habitats (Lambers and Poorter 1992, Grime et al. 1997). Studies also suggest that faster growing plants are more plastic in their growth responses than slower growing plants, and that LAR and specific leaf area (SLA, leaf area per unit leaf biomass) are the most important factors controlling growth rate (Grime et al. 1986, Lambers and Dijkstra 1987, Poorter 1989, Lambers and Poorter 1992).

Betula under control conditions has smaller ramets and a smaller relative growth rate in length than does *Salix,* while its SLA is similar to that of *Salix.* In addition, *Betula* invests considerably more in secondary metabolites (Bryant et al. 1989) and lignin (Hobbie 1996) than *Salix* does. These investments in nonphotosynthetic structure should reduce *Betula*'s growth rate and hence its growth plasticity (Lambers and Dijkstra 1987, Poorter 1989, Lambers and Poorter 1992). Thus, *Betula*'s superior plasticity under fertilization seems contrary to generalizations that SLA or growth rate under control conditions predicts growth plasticity. We suggest that in this ecosystem, meristem availability is a better predictor of growth plasticity under fertilization than is the relative growth rate, LAR, or SLA of plants under control conditions.

Meristem availability is not usually considered in ecological theories of controls over allocation of resources to different plant organs as a determinant of plant growth (e.g., Reynolds and Thornley 1982, Chapin et al. 1987, Garnier 1991, Hilbert and Reynolds 1991, Rastetter and Shaver 1992). However, availability of meristems has been demonstrated to affect plant size (Watson 1984) and fecundity (Geber 1990), and has been proposed to limit growth in some cases (Körner 1991). A rigidly controlled program of meristem activity may mean that available carbon will not all be used for growth, which will cause physiological regulation to reduce photosynthetic assimilation (Quick et al. 1991, Krapp and Stitt 1995). Coleman and Jones (1991) also suggested that differences in patterns of plant development may account for otherwise inexplicable variations in plant responses to, and effectiveness of plant defense against, herbivory. The present study provides an example of meristem availability affecting plant growth response to altered environmental conditions.

The availability of active meristems will limit plant growth response to improved environmental conditions when either (1) the activity of existing meristems to produce more leaves cannot be increased substantially, or (2) increasing the activity of existing meristems has a small effect relative to increasing the number of meristems. We suggest that meristem availability is likely to be particularly important in controlling plant response to changed conditions in ecosystems where the growing season is short, where many plants have determinate shoots, or where a high proportion of yearly plant growth is derived from preformed buds. Most arctic and alpine plants grow from preformed buds (Aydelotte and Diggle 1997, Diggle 1997). Thus, availability of active meristems may be useful for predicting plant response to altered environmental conditions in other ecosystems where any of the above conditions are met.

Consequences of individual growth for community structure

Our results, when combined with those of previous research at the same site (Shaver and Chapin 1980, Chapin and Shaver 1985, Chapin et al. 1995, Chapin and Shaver 1996), suggest that declines in the biomass of *Ledum* and *Salix* under fertilization may be due to decreased light availability caused by *Betula*'s extensive upward growth and branching. This has created a much taller and denser canopy than previously existed and now shades the other vegetation (Table 5).

Ledum is at or near the top of the low, sparse canopy

in the control plots, but has become largely confined to the understory in fertilized plots. From net photosynthesis vs. light intensity curves on control *Ledum* ramets (M. S. Bret-Harte, *unpublished data*), we calculate that the light intensity measured in the understory of the two fertilized treatments is low enough to reduce *Ledum*'s net photosynthetic rate to only 5% of its net photosynthetic rate at the light intensity in the understory of control plots (Table 5). This would seriously impact *Ledum*'s carbon economy during the period when *Betula* has leaves, even if *Ledum* were able to alter its leaves' photosynthetic characteristics to become those of shade leaves, as changes in the morphology of its leaves (larger, thinner, fully unrolled) suggest. Stems of *Ledum* are weak and sprawling, because it has very little secondary growth (Shaver 1986). Thus *Ledum* cannot grow tall enough to compete for light with the tall, dense *Betula* canopy. Although *Salix* ramets are tall enough to reach the top of the canopy in the fertilizer treatments, buds growing from shoot bases would receive little light. Because *Salix* loses the apical parts of its shoots fairly often because of winter death or herbivory, this light environment could reduce regrowth from buds lower on the plant. Plant production in the understory of this fertilized ecosystem may be changing from being limited primarily by nutrient availability to being limited by light availability.

Acknowledgments

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