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SPECIES COMPOSITION INTERACTS WITH FERTILIZER TO CONTROL LONG-TERM CHANGE IN TUNDRA PRODUCTIVITY

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Abstract. Fifteen years of N and P fertilizer addition to an Alaskan moist tundra increased aboveground biomass and primary production by 2.5 times. Species composition of the fertilized vegetation also changed dramatically, from a mix of graminoid, evergreen, deciduous, and moss species to strong dominance by a single, deciduous shrub species, *Betula nana.* Analysis of these simultaneous changes allows insights into the interactions between changes in resource availability and changes in species composition in regulating vegetation biomass, production, and element use.

By the 15th year (1995), both new leaf production and total leaf mass were *lower* in fertilized than in control plots, although leaf area in fertilized plots was twice that of controls. This occurred because *Betula* produced thinner leaves than other species, with a high specific leaf area (SLA, leaf area per unit leaf mass). Woody stem mass also increased dramatically in fertilized plots, with secondary growth accounting for over half of aboveground net primary production, NPP. The large increase in wood production was made possible, in part, by the low cost of production of *Betula*'s thin leaves, allowing greater allocation to secondary growth. Wood also had lower N concentrations than leaves, allowing large accumulations of wood at low N cost. Overall, aboveground N concentration in *Betula* did not change in fertilized relative to control plots, because its low-N wood mass increased more than its high-N leaf mass (with high SLA). Because *Betula* was so strongly dominant on the fertilized plots and was better able to dilute its greater N supply with new growth, community production and biomass in fertilized plots were higher, and N concentration was lower, than would have been the case if species composition had not changed.

Aboveground biomass and leaf area of individual species and functional types were predicted accurately by regression against the number of hits per point-frame pin across the full range of data, including both treatments. Changes in overall canopy structure and leaf display due to fertilization were thus due mainly to changes in species composition, with no detectable effect of treatment on size/structure relationships within species or functional types.

Key words: allocation; Arctic; biomass; Brooks Range, Alaska; fertilizer; nutrients; primary production; secondary growth; species composition; specific leaf area; tundra productivity.

INTRODUCTION

Environment and species composition are both changing rapidly in many parts of the world, largely as a direct or indirect result of human activities. To understand how these changes interact with each other to control important ecosystem processes like primary production and organic matter cycling, we need to document the changes as they occur and to compare the changes in environment, species composition, and ecosystem processes over time. Often the best way to do this is in a long-term ecosystem-level experiment, in which the environment or species composition is manipulated in a controlled fashion to illuminate a clear chain of cause–effect relationships. Long-term experiments in ecology often lead to conclusions that never would have been predicted from the initial responses to a given manipulation (Likens 1989, Magnuson 1990, Powell and Steele 1995). Variable response times, buffered responses, and feedbacks among different components of the ecosystem all combine to confound predictions based on apparently simple initial cause–effect relationships. Thus, long-term observation and experimentation are essential to improve long-term predictions of ecological change.

The aim of this paper is to describe 15 yr of change in composition, biomass, and productivity of moist tussock tundra, in response to an annual N + P fertilizer treatment at Toolik Lake, on the North Slope of Alaska. The changes after three and nine years have been described previously (Chapin et al. 1995, Chapin and Shaver 1996, McKane et al. 1997). An analysis after 15 yr provides the opportunity to determine whether

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the pace of long-term change has slowed, and whether any new, qualitatively different changes have developed since the earlier harvests of this experiment. In particular, this analysis focuses on the effects of changes in species composition and the relative abundance of plant functional types in the vegetation. In an experiment in which fertilizer addition has caused clear and dramatic changes in species composition, vegetation biomass, and productivity, we ask (1) whether the changes in biomass and production were due solely to the fertilizer addition, irrespective of species composition; or (2) whether the changes in species composition had a measurable, additional effect on biomass and production.

Effects of individual species or functional types on ecosystem biogeochemistry are currently the subject of intense debate (e.g., Naeem et al. 1999, Kaiser 2000, Naeem 2000, Wardle et al. 2000). This issue also has a long history of research in the Arctic, with an emphasis on species–nutrient interactions and especially species–N interactions (Berendse and Jonasson 1992, Hobbie 1995, Shaver 1995, Chapin et al. 1996, Shaver et al. 1996). A focus on the N cycle is based on the repeated demonstration that production and biomass accumulation in arctic tundras are strongly nutrient limited, usually by N in relatively well-drained moist tundras such as the site used in this study (Shaver et al. 1986, Shaver and Chapin 1995, Jonasson et al. 1996). During the 1970s, a number of ecologists observed that more productive tundra sites tend to be dominated by rapidly growing species with high N uptake rates, but also with high rates of biomass turnover (especially of leaves) and high leaf nutrient concentrations (e.g., Chapin et al. 1980, Miller et al. 1984). Deciduous woody shrubs, such as *Betula nana* and *Salix* species, were particularly dominant in the most productive sites. Yet, despite the high leaf turnover and high leaf nutrient concentrations in these species, deciduous shrubs were able to accumulate high total biomass because most of their biomass was wood, which has relatively low concentrations of the most limiting elements, N and/or P (Shaver and Chapin 1991). More recent research has shown that species composition of tundras may have a number of additional effects on overall N cycling, including effects related to litter decomposition and N mineralization (Hobbie 1996), to variable capacity for N uptake from different sources in the soil (Michelsen et al. 1996, 1998, Nadelhoffer et al. 1996), and to variable capacity for rapid growth in response to change in N availability (Bret-Harte et al. 2001).

In the present study, we extended these earlier studies by focusing on leaf vs. stem allocation and by exploring various measures of production ''efficiency,'' i.e., primary production per unit biomass, N mass, leaf mass, leaf area, or leaf N content. Past work has already shown that leaf N allocation in arctic tundras is a critical control over canopy-level photosynthesis (Williams and Rastetter 1999, Williams et al. 2001). Our data set allows us to determine how changes in species composition in response to fertilizer addition over a period of 15 yr have led to changes in N allocation and N use at the level of the whole vegetation that allows higher productivity than would be possible if species composition remained constant.

Site and Experimental Design

Toolik Lake is located in the northern foothills of the Brooks Range, Alaska, USA (68°38′ N, 149°34′ W; elevation 760 m). The area around the lake has been studied intensively since the construction of the Dalton Highway and Alyeska Oil Pipeline in 1975–1976; it is now part of the U.S. network of Long Term Ecological Research sites (Hobbie et al. 1994, Shaver 1996). Vegetation of the area is typical of the North Slope foothills region (Walker et al. 1989), and detailed studies of production, biomass, and element cycles of the major vegetation types have been completed (Giblin et al. 1991, Shaver and Chapin 1991, Shaver et al. 1996).

The vegetation chosen for study in this work is moist acidic tussock tundra, dominated by the sedge *Eriophorum vaginatum.* Moist acidic tussock tundra is one of the most common arctic vegetation types, in both North America and Eurasia (Bliss and Matveyeva 1992). Although *E. vaginatum* dominates by controlling microtopography and surface microclimate (Chapin et al. 1979), deciduous and evergreen shrubs (*Betula nana, Ledum palustre, Vaccinium vitis-idaea*) are roughly equal in abundance, with mosses forming a nearly continuous surface cover (Shaver and Chapin 1991).

Numerous experiments, some with fertilizer treatments, have shown that productivity of tussock tundra is usually N limited, although P limitation and K limitation have also been demonstrated at some sites (Shaver and Chapin 1995). Productivity at the Toolik Lake site is N limited (Shaver et al. 1986), and the N limitation is much stronger than potential limitation by low light or low temperature (Chapin et al. 1995). In fertilizer experiments, however, we frequently find a secondary P limitation in plots fertilized with N (e.g., Shaver and Chapin 1980, Shaver et al. 1986), so we normally add both N and P fertilizers together. In the present paper, we focus only on the N response and on N uptake and allocation; uptake and allocation of P in earlier harvests of the same experiment were described in several previous papers (e.g., Chapin et al. 1995, Chapin and Shaver 1996). We have evaluated the N × P interaction in over a dozen previous experiments in both wet and moist tussock sites in Alaska (Shaver and Chapin 1995), including an earlier experiment at this site (Shaver et al. 1986).

The present experiment was begun in June 1981 and originally included manipulations of air temperature using small greenhouses and light by artificial shading, as well as N + P fertilizer addition (Chapin et al. 1995,

Chapin and Shaver 1996). After harvests in 1983 and 1989, the greenhouse and shade treatments were discontinued, but annual fertilizer addition was maintained. The fertilized plots received 10 g $P \cdot m^{-2} \cdot yr^{-1}$ N as NH_4NO_3 and 5 g $N \cdot m^{-2} \cdot yr^{-1}$ P as P_2O_5, in the form of granular agricultural fertilizer. The fertilizer was added each May or June from 1981 to 1995, as soon as the investigators arrived at the site each summer and the site was snow free. Details of the experimental design and treatment effects on environment are provided in Chapin et al. (1995).

The experimental layout consisted of four large, replicate blocks of moist tussock tundra, each block containing four 5 × 20 m plots arranged parallel to each other with 1 m wide buffer strips between them. Treatments, including the control and fertilized plots described here, were assigned randomly to one plot within each block. Extensive prior experience with similar experiments at other Alaskan sites (including 11 other tussock tundra sites; Shaver and Chapin 1995) showed that four large, replicate plots, with 3–5 samples collected from each plot, were sufficient to detect highly significant responses.

Methods

Quadrat location and selection

In late July–early August 1995, in each of the four control and fertilized plots, we intensively sampled five 20 × 20 cm quadrats. The five quadrats in each plot were located at random along 20-m transects placed 1 m from the eastern edge of the 5 × 20 m plots. The transects were located at the eastern edge of each plot because sampling in earlier years had started at the western edge and gradually moved eastward, with the aim of avoiding sampling in locations that had previously been sampled or trampled. Once the quadrat locations were determined, the corners were marked while sampling took place over the next 7–10 d.

Point-intercept sampling

Four of the five quadrats in each treatment and block were selected at random for point-intercept sampling (Jonasson 1983, 1988, Hobbie et al. 1999). Our aim in using this method was simply to determine the relationship between the number of pin contacts and biomass or leaf area measurements obtained by clip harvest of the same quadrat, *not* to obtain an independent, direct estimate of leaf area index. To determine the correlation with clip harvest data, quadrats were sampled using a frame containing a grid of points 2.5 cm apart, for a total of 64 points in a 20 × 20 cm quadrat. A metal rod (5 mm = 3/16 inch diameter) was dropped vertically through the vegetation at each sample point. All hits of vegetation by the rod were recorded by species and tissue type, from the top of the canopy to the soil or moss surface.

Biomass, leaf area, and N content

After the point-intercept sampling was completed, live aboveground biomass was collected from each quadrat by clipping with scissors or knives. All samples were collected between 31 July and 2 August and were sorted within 48 h of collection. The samples included all vascular plants, green portions of the surface moss layer, and living lichen tissue within the quadrat. Sorting and analysis of these samples was identical to methods used in previous harvests of this experiment, so that results from 1995 could be compared directly with those from 1982 (Shaver and Chapin 1991), 1983 and 1989 (Chapin et al. 1995), and 1984 (G. R. Shaver and F. S. Chapin, *unpublished data*). The only differences among the harvests were that (1) the earlier harvests included belowground stems and rhizomes, whereas we harvested only aboveground parts in 1995; (2) mosses were sampled only in 1982, 1989, and 1995; and (3) leaf area was measured only in 1982 and 1995.

In the field laboratory at Toolik Lake, the live biomass from each quadrat was first sorted by plant functional type (graminoid, deciduous shrub, evergreen, forb, moss, or lichen). Within each functional type, the most abundant two or three species were separated individually, with less abundant species lumped for biomass determination after species identity was recorded. Each vascular species (or species group for the less abundant species within each growth form) was then separated into several tissue categories including current year's vs. previous years' leaves, current year's vs. previous years' stems, and inflorescences. All leaf samples were run through a LI-COR leaf area meter (Model LI-3000A; LI-COR Instruments, Lincoln, Nebraska, USA) for determination of leaf area before drying. Moss and lichen tissues were not separated beyond the species or species group. All tissues were then dried for several days at 50–60°C in a field drying oven, and weighed.

In our Woods Hole, Massachusetts, USA laboratory, the dried samples were analyzed for total N content in a Perkin-Elmer CHN analyzer (Perkin-Elmer Instruments, Norwalk, Connecticut, USA). As in our previous research (Shaver and Chapin 1991, Chapin et al. 1995), the samples from individual quadrats were lumped by block, so there was only one lumped sample from each block that was analyzed for N content (i.e., $n = 4$ samples per species, tissue, and treatment).

Primary production: apical growth and secondary stem growth

Aboveground vascular net primary production (ANPP) was estimated as the sum of the current year's apical and secondary growth. Apical growth was defined as that produced from apical or intercalary meristems during the current growing season; it was calculated by our standard method of summing the masses of all current year's leaf, stem, and inflorescence tissues

in the quadrat harvest (Shaver and Chapin 1991, Chapin et al. 1995). Secondary growth was calculated as a percentage of the old live woody stem mass (Shaver 1986), using new estimates of annual secondary growth rate (in percentage per year) that were obtained from a separate, detailed analysis of woody shrub growth (Bret-Harte et al. 2001; M. S. Bret-Harte and G. R. Shaver, *unpublished data*).

Secondary growth (wood production) is important for only three species in the vegetation at this site: *Ledum palustre*, *Salix pulchra*, and *Betula nana*. For *Ledum* and *Salix*, estimates of secondary growth rates in both control and fertilized plots were available from previous research on the same site at Toolik Lake (Chapin et al. 1995; G. R. Shaver, *unpublished data*). For *Betula nana*, however, previous estimates of secondary growth were not available because *Betula* does not produce the distinct annual bud scars that were used for determination of stem age in *Ledum* and *Salix*. In past research (Shaver and Chapin 1991, Chapin et al. 1995), we assumed that secondary growth by *Betula* was the same as that of *Salix* (both are woody deciduous shrubs). By 1995, however, *Betula* had become so dominant on the fertilized plots and was growing so much more rapidly than the other species that we clearly needed a separate measure of its secondary growth.

In 1995 and 1996, we completed a new analysis of secondary growth in all three dominant woody species (*Betula*, *Ledum*, and *Salix*) on a separate set of fertilized and control plots ~1 km away from the present study site (Bret-Harte et al. 2001; M. S. Bret-Harte and G. R. Shaver, *unpublished data*). A detailed presentation of our results is beyond the scope of this paper, but the method was similar to the one that we have used previously (Shaver 1986). Briefly, to determine stem age in *Betula*, we used thin sections of stems, cut freehand with a razor and stained with phloroglucinol (1% mass per volume in 20% HCl). Annual growth rings in the stained sections were counted under a microscope. Stem ages of the other two species were determined as previously, by counting annual bud scars back from the apex with occasional ring counts for verification. We collected segments of varying ages by random collection of large branches, separating the segments of each branch by age. We then dried the segments, and weighed and measured the length of each segment age class separately. Secondary growth rates (percentage per year) for the whole branches were then calculated from a regression of stem mass per unit length against segment age and from the numbers, mass values, and lengths of segments of each age class (M. S. Bret-Harte and G. R. Shaver, *unpublished data*).

The secondary growth rates that we used in the present study for calculation of the secondary growth component of primary production are presented in Table 1. For unfertilized control plants, the new estimates of secondary growth rates were similar to those of Shaver (1986), ranging from 7.9% per year in *Ledum palustre* in the present study to 18.1% per year in *Salix pulchra*. In the control plots, secondary growth of *Betula nana* (15.8% per year) was quite similar to our previous, assumed growth rate of 15.5% per year. In the fertilizer treatment, though, the new estimates showed a substantial increase in secondary growth relative to controls, especially in *Betula* (Table 1).

TABLE 1. Secondary growth rates of woody stem mass in three shrub species in control and fertilized plots at Toolik Lake, Alaska, USA.

Species	Annual growth rate of woody stem mass (%)	
	Control	Fertilized
Ledum palustre	7.9	20.3
Salix pulchra	18.1	25.1
Betula nana	15.8	44.1

Note: Information in this table is from M. S. Bret-Harte and G. R. Shaver, *unpublished data.*

Data analysis

Data were analyzed statistically using SYSTAT 8.0 (SPSS 1998) and SAS Version 8.0 for Windows (SAS Institute 1999). Because the data on production, biomass, and N content did not deviate markedly from assumptions of normality and homogeneity of variance, these analyses were completed using untransformed data. The appropriate ANOVA (GLM) design for treatment effects in such an experiment is a one-way, complete-block design with blocks as replicates ($n = 4$ blocks in this experiment) and individual samples nested within blocks ($n = 5$ quadrats per block for biomass/NPP harvests). When samples are compared among years, this becomes a repeated-measures design (e.g., Chapin et al. 1995). We also used simple correlation analyses to examine relationships between variables on a quadrat-by-quadrat basis, and analysis of covariance (ANCOVA) to compare regression slopes between treatments. In the correlation analyses and ANCOVAs, we ignored block effects because they were never significant.

RESULTS

Species composition and aboveground biomass

In the 1995 (15-yr) harvest, the fertilizer treatment contained both fewer vascular plant species overall (i.e., it had lower species *richness*, the cumulative number of species observed in all quadrats) and fewer species per quadrat and per block (i.e., lower species *density*, the average number of species in a sample of constant area) than did the control. For overall species richness, the numbers from 1995 were similar to those from the 1983 or 1989 harvests. In all three of these years, a total of 15 or 16 vascular species was found in quadrats from control plots vs. a total of 11–14 species in fertilized plots (Tables 2 and 3). In 1995, there were five common species that typically appeared in

TABLE 2. Species present in control and fertilized tussock tundra plots in 1995. Within each growth form, species are arranged in order of decreasing abundance in control plots.

Growth form and species	Control	Fertilized
Graminoids	*Eriophorum vaginatum* *Carex bigelowii* *Arctagrostis latifolia*	*Eriophorum vaginatum* *Carex bigelowii* *Calamagrostis holmii* *Arctagrostis latifolia* *Eriophorum angustifolium*
Deciduous	*Betula nana* *Salix pulchra* *Rubus chamaemorus* *Vaccinium uliginosum* *Arctostaphylos alpina*	*Betula nana* *Salix pulchra* *Rubus chamaemorus*
Evergreen	*Ledum palustre* *Vaccinium vitis-idaea* *Empetrum nigrum* *Andromeda polifolia* *Cassiope tetragona*	*Ledum palustre* *Vaccinium vitis-idaea* *Empetrum nigrum*
Forbs	*Polygonum bistorta*† *Pedicularis* sp. *Petasites frigidus*†	*Polygonum bistorta*† *Stellaria crassifolia*

† Species not found in quadrat samples but observed in plots.

≥10% of the control quadrats but were not found in the fertilized quadrats: *Vaccinium uliginosum, Arctostaphylos alpina, Andromeda polifolia, Cassiope tetragona,* and *Pedicularis* spp. (the *Pedicularis* in the control plots was mainly *P. lanata,* but may have included small, nonflowering individuals of *P. lapponica, P. labradorica,* or *P. capitata*). The 1995 harvest was the first time that fertilized plots contained two species not found in controls (*Eriophorum angustifolium* and *Stellaria crassifolia*), but these were found in only one or two of the 20 quadrats harvested, and both species were observed in control plots in previous years.

Species density at the quadrat scale (0.04 m^2) was reduced significantly by fertilizer treatment ($P < 0.0001$). Species density also decreased in 1995 in comparison to earlier harvests (year effect significant at $P = 0.005$), and the difference in species density between control and fertilized plots tended to increase over time, although the year × treatment interaction term was only moderately significant ($P = 0.09$). This result was driven by a significant interaction between year and treatment between 1983 and 1989 ($P = 0.04$), whereas there was no significant interaction between year and treatment between 1989 and 1995 ($P > 0.1$). There were about seven vascular species in each control quadrat in 1983, 1989, and 1995, whereas the mean number of vascular species in fertilized quadrats declined from 6.05 in 1983 to 4.55 in 1995 (Table 3). At the block level, there were 11–12 species per five quadrats (0.2 m^2) in control plots and 8–9 species per five quadrats in fertilized plots (treatment effect significant at $P < 0.02$, no significant interaction term or year effect). This pattern of relatively constant overall species richness over time in both control and fertilized plots, vs. a tendency for continued decreases in species density, especially in fertilized plots at the finest sampling scale, suggests that 2–4 poorly competitive species were eliminated almost immediately from the fertilizer treatment (in 1981 or 1982), followed by gradually increasing dominance of the remaining species by those species that were most favored by fertilization. Similar reductions in species richness or density have been reported in fertilizer experiments in a wide range of herbaceous plant communities (Gough et al. 2000).

TABLE 3. Species density (mean ± 1 SE), for vascular species only, among individual quadrats ($n = 20$) and among blocks ($n = 4$, lumping the five quadrats from each block), and overall species richness (total number of species, lumping all quadrats; $n = 1$), in control and fertilized tussock tundra plots in 1995.

Treatment and year	Quadrats (No. species/ 0.04 m^2)	Blocks (No. species/ 0.2 m^2)	Overall richness (No. species/0.8 m^2)
Control			
1983	7.15 ± 0.34	11.25 ± 0.75	15
1989	7.15 ± 0.46	12.00 ± 1.22	16
1995	6.75 ± 0.25	11.00 ± 1.29	16
Fertilized			
1983	6.05 ± 0.25	9.00 ± 0.71	12
1989	5.40 ± 0.34	8.75 ± 0.25	14
1995	4.55 ± 0.34	8.00 ± 0.41	11

The increasing dominance by one species, *Betula nana,* in the fertilized plots is most clearly shown in a plot of each species' relative biomass vs. its rank in order of biomass (Fig. 1). In control plots, there were always the same three or four species (*Eriophorum vaginatum, Ledum palustre, Vaccinium vitis-idaea,* and *Betula nana*) that had similar biomass, although their relative abundance differed from year to year. At all

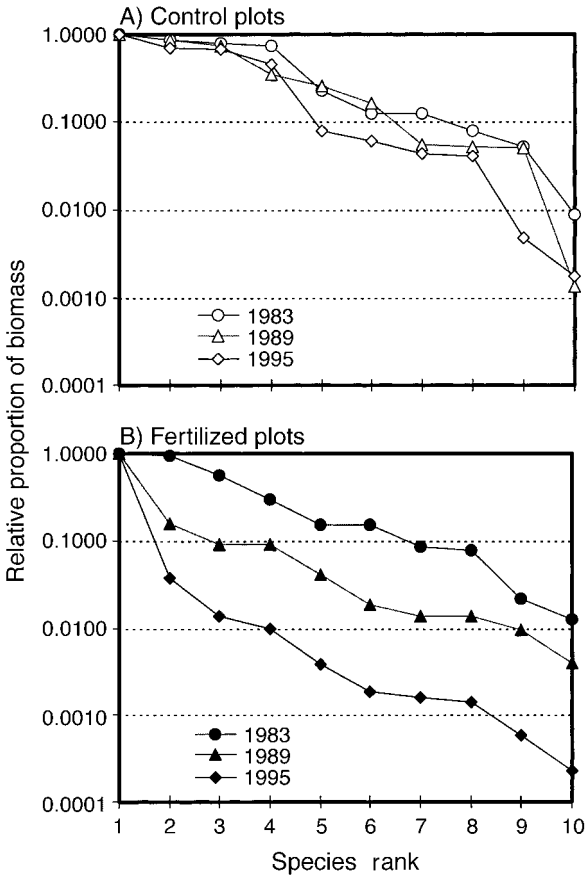

FIG. 1. Species rank–abundance curves for aboveground vascular plant biomass in (A) control and (B) fertilized plots in 1983, 1989, and 1995. Each point represents one vascular plant species, ranked in order of decreasing biomass on the horizontal axis and with biomass as a proportion of the biomass of the most abundant species on the vertical axis (note the log scale). Data points were calculated from mean biomass values for each species, treatment, and year; thus, confidence intervals cannot be calculated.

harvests, it was not until the ninth or tenth species was reached that biomass dropped below 1% of the most abundant species. In fertilized plots, on the other hand, the slope of this relationship was similar to that of the control plots in the early years of the experiment, but dominance became more pronounced with each successive harvest. By 1995, the second most abundant species in the fertilized plots, *Ledum palustre,* had only ~4% of the biomass of *Betula nana;* all species after the fourth most abundant (''other graminoids,'' mainly *Calamagrostis holmii* and *Arctagrostis latifolia*) had <1% of *Betula*'s biomass.

Total aboveground vascular biomass in control plots was 316 ± 23 g/m^2 in 1995, a marginally significant increase of 63 g/m^2 since 1989 ($P = 0.06$), but near the middle of the range among the five measurements since 1982 (Fig. 2A; year effect significant at $P = 0.007$). Over 50% of the total aboveground biomass in 1995 consisted of the evergreen species *Ledum palustre* and *Vaccinium vitis-idaea,* ~15% was *Eriophorum vaginatum,* and ~20% was *Betula nana.* The relative abundances of these species changed considerably from 1982 to 1995, due to a large increase in the abundance of *Ledum palustre* and a decrease in *Eriophorum vaginatum* (Fig. 3A). Since the first sampling in 1982 (Shaver and Chapin 1991), aboveground biomass of all graminoids declined from 25–30% of the community total to 15–20% in 1995 (because these data include aboveground parts only, the relative importance of graminoids appears much less than would be the case if belowground stems and rhizomes were included). The two dominant evergreen species, on the other hand, increased in relative abundance from ~35% of the total in 1982 to ~55% in 1995, whereas the deciduous species were relatively constant, at ~25% of total aboveground vascular biomass.

In the fertilized plots, on the other hand, there were dramatic changes over the 15-yr period in both aboveground biomass and species composition relative to control plots (Fig. 2B; year effect significant at $P < 0.0001$). By 1995, total aboveground biomass of fertilized plots was 803 ± 92 g/m^2, over 2.5 times that of control plots ($P < 0.0001$) and an increase of >50% from the 1989 value of 516 g/m^2 ($P = 0.008$). By 1995,

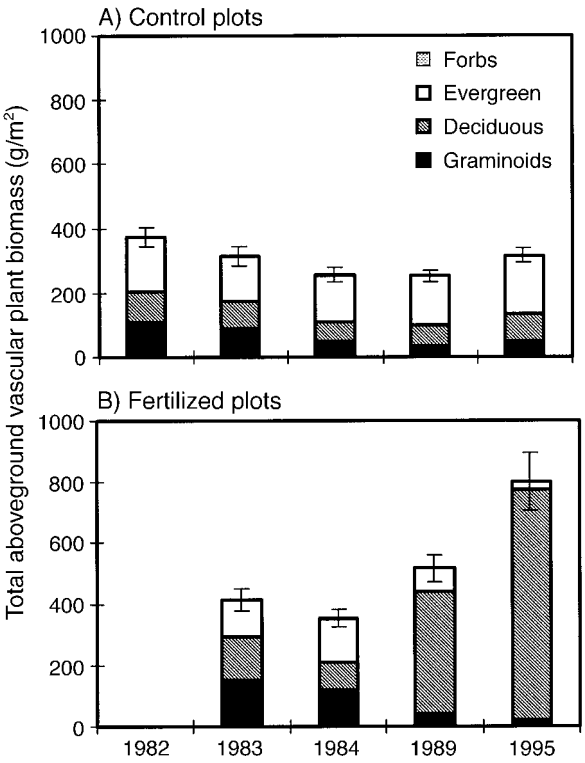

FIG. 2. Total aboveground vascular biomass (mean ± 1 SE) in (A) control and (B) fertilized plots, 1982–1995. The segments of each bar indicate aboveground biomass of each of the four major growth forms, with forb biomass included, but always too small to be seen at this scale.

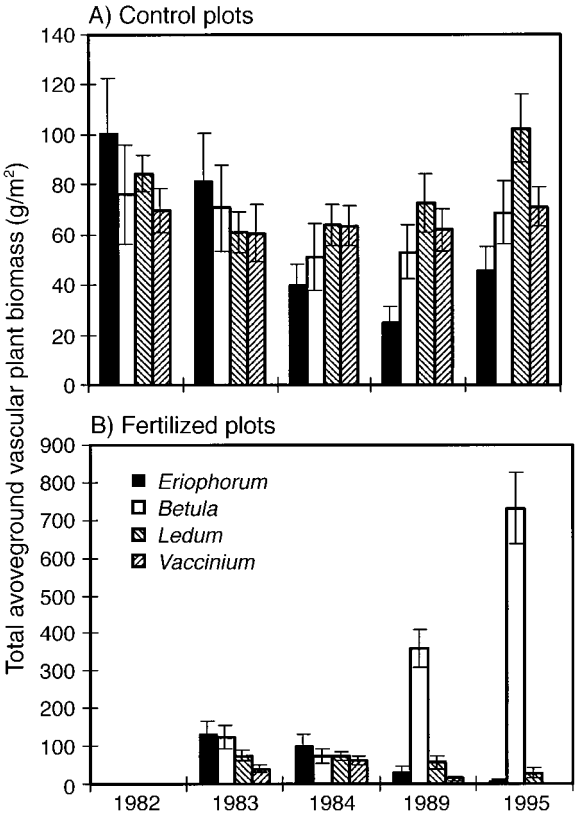

FIG. 3. Total aboveground biomass (mean ± 1 SE) of four dominant vascular species in (A) control plots and (B) fertilized plots, 1992–1995.

Betula nana biomass had increased more than 10-fold relative to controls ($P < 0.0001$), and accounted for 90% of total vascular aboveground biomass in fertilized plots (Table 4), an increase from 70% in 1989. The other species that shared dominance in control plots continued to decline in importance (Fig. 3B). Only *Betula nana, Rubus chamaemorus,* ''other graminoids'' (mainly *Calamagrostis holmii* and *Arctagrostis latifolia*), and forbs had higher biomass in fertilized than in control plots (Table 4). These differences were highly significant ($P < 0.001$) except for ''other graminoids'' ($P < 0.17$) and forbs.

Moss and lichen biomass were significantly lower in 1995 than in 1989 in both control and fertilized plots ($P < 0.001$ and $P < 0.05$, respectively), continuing the long-term declines that we observed in both treatments between 1983 and 1989 (Chapin et al. 1995). In the fertilized plots, the decline in mosses and lichens was probably caused by shading at the soil surface due to increased *B. nana* canopy growth, and by increased leaf litter fall (accumulated leaf litter was >5 cm thick in some locations beneath fertilized *B. nana*). By 1995, mosses and lichens in the fertilized plots were almost completely eliminated from the vegetation (Table 4). The continued decline in moss and lichen mass in control plots through 1995 might reflect increased shading by evergreen shrubs (Fig. 2) or the generally warmer, drier conditions of the previous 15 yr (Chapman and Walsh 1993). By 1995, the total moss plus lichen biomass in control plots was less than half that in any previous year (Shaver and Chapin 1991, Chapin et al. 1995), but still two orders of magnitude greater than on the fertilized plots (treatment effect for 1995 significant at $P < 0.0001$).

Aboveground primary production

Aboveground vascular production of control plots was 145 g/m² in 1995, an increase of 40 g/m² from 1989 ($P < 0.011$), but still less than the production that was measured in 1982 or 1983 (Fig. 4A; year effect significant at $P < 0.007$). Overall, aboveground production varied by almost 80% from the least productive year (1984) to the most productive year (1982). This variation in production was greater than the 50% variation in aboveground biomass among years (Fig. 2A), and was due primarily to large decreases in *Eriophorum* production from 1982 to 1984, and to increases in both *Eriophorum* and *Ledum* production from 1989 to 1995. In all years, stem secondary growth in control plots was only a small component of aboveground production (e.g., 13 ± 1 g/m² vs. 132 ± 9 g/m² for apical growth in 1995); ~60–70% of this secondary growth was by deciduous species (mainly *Betula*), and ~30–40% was by evergreens (mainly *Ledum*).

In the fertilized plots in 1995, aboveground vascular production was 350 g/m², more than double that in control plots ($P < 0.0001$; Table 4, Fig. 4B). Of this total, 196 g/m² (56%) was secondary growth, nearly all of it by *Betula*. Total production by *Betula* alone was 297 g/m², or 85% of the community total. This dominance by *Betula* in the fertilized plots began to develop as early as 1984, with evergreen shrubs and forbs being almost completely eliminated by 1995 (Figs. 2B and 3B). Current year's apical growth also decreased significantly over time in the fertilized plots, from 238 g/m² in 1983 to 154 g/m² in 1995 ($P < 0.05$), whereas secondary growth increased sixfold from 28 g/m² to 196 g/m² ($P < 0.0001$).

Because the increases in secondary growth tended to compensate for the decreases in apical growth and in production of nonwoody species, the relative year-to-year variation in total aboveground production was much less in fertilized plots than in controls, with an increase of only 132 g/m² (61%) from the least productive (1984) to the most productive (1995) year ($P < 0.01$). The fertilizer plots were still more productive than controls in every year, with production in fertilized plots relative to controls tending to increase over time; i.e., the relative increase in production in fertilized plots relative to controls was 1.7-fold in 1983, 2.1-fold in 1984, 2.6-fold in 1989, and 2.4-fold in 1995.

TABLE 4. (A) Aboveground biomass (g/m^2) and (B) primary production ($g \cdot m^{-2} \cdot yr^{-1}$), by species and growth form, in the 1995 harvest of control and fertilized plots at Toolik Lake, Alaska. Values are means ± 1 SE.

Growth form, species, and type of production	Control	Fertilized
A) Aboveground biomass		
Graminoid		
Eriophorum vaginatum	46.12 ± 8.84	7.12 ± 3.58
Carex bigelowii	4.15 ± 1.61	2.79 ± 1.35
Other graminoid species	1.05 ± 0.66	10.15 ± 6.52
Deciduous		
Betula nana	68.83 ± 12.22	730.68 ± 94.29
Salix pulchra	6.14 ± 4.24	1.16 ± 0.83
Rubus chamaemorus	0.18 ± 0.18	20.45 ± 4.20
Vaccinium uliginosum	0.03 ± 0.03	0.00 ± 0.00
Other deciduous species	4.48 ± 4.48	0.00 ± 0.00
Evergeen		
Ledum palustre	102.45 ± 13.71	27.77 ± 13.48
Vaccinium vitis-idaea	71.09 ± 7.85	1.04 ± 0.49
Other evergreen species	8.04 ± 2.54	0.43 ± 0.42
Forb species	0.49 ± 0.20	1.35 ± 1.05
Moss species	111.84 ± 16.67	0.88 ± 0.42
Lichen species	15.96 ± 4.01	0.12 ± 0.06
Total for each growth form		
Graminoid	51.33 ± 9.09	20.06 ± 7.06
Deciduous	82.45 ± 12.20	752.29 ± 94.36
Evergreen	181.58 ± 18.61	29.24 ± 14.09
Vascular	315.84 ± 22.96	802.93 ± 92.32
Nonvascular	127.79 ± 15.76	1.00 ± 0.43
Vascular plus nonvascular	443.64 ± 18.13	803.93 ± 92.21
B) Aboveground primary production		
Apical growth		
Graminoid	51.33 ± 9.09	20.06 ± 7.06
Deciduous	26.93 ± 4.22	126.97 ± 11.95
Evergreen	53.74 ± 4.48	5.93 ± 2.43
Forb	0.49 ± 0.20	1.35 ± 1.05
Total vascular	132.49 ± 8.88	154.30 ± 9.36
Secondary growth		
Deciduous	7.65 ± 1.24	192.38 ± 26.78
Evergreen	5.27 ± 0.66	3.20 ± 1.74
Total vascular	12.92 ± 1.44	195.58 ± 26.92
Total ANPP		
Graminoid	51.33 ± 9.09	20.06 ± 7.06
Deciduous	34.58 ± 5.13	319.35 ± 35.08
Evergreen	59.01 ± 4.98	9.13 ± 4.04
Forb	0.49 ± 0.20	1.35 ± 1.05
Total vascular	145.41 ± 9.45	349.88 ± 31.59

Leaf area, leaf mass, and specific leaf area

Total vascular leaf area in the fertilized plots in 1995 was 1.94 m^2 leaf per m^2 ground, or double that of the controls (0.97 m^2/m^2; Table 5). This doubling of leaf area due to fertilization ($P < 0.0001$) was slightly less than the 2.4-fold difference in aboveground vascular production and the 2.5-fold difference in aboveground biomass (Table 4; both $P < 0.0001$). Leaf area of individual species and growth forms also increased when their production and biomass increased, and vice versa, although leaf area, production, and biomass did not always change by the same proportions (Tables 4 and 5).

Total vascular leaf mass, on the other hand, was 20% *lower* in fertilized than in control plots in 1995 (119 vs. 151 g/m^2, $P < 0.03$; Table 5). This decrease in leaf mass, in contrast to the increase in leaf area, was due mainly to the dominance of *Betula* and *Rubus* in fertilized plots. These two species had a much higher specific leaf area (SLA, in centimeters of leaf area per gram of leaf mass) than did any of the evergreen or graminoid species that dominated in control plots (Table 5). The fertilizer treatment also caused SLA to increase by 10–40% within every species present (although most of these within-species increases in SLA were not significant), so that overall SLA more than doubled for the community as a whole ($P < 0.001$).

Nitrogen content and allocation

In 1995, total aboveground vascular N stocks in fertilized plots were 9.6 g/m^2, a 2.4-fold increase over

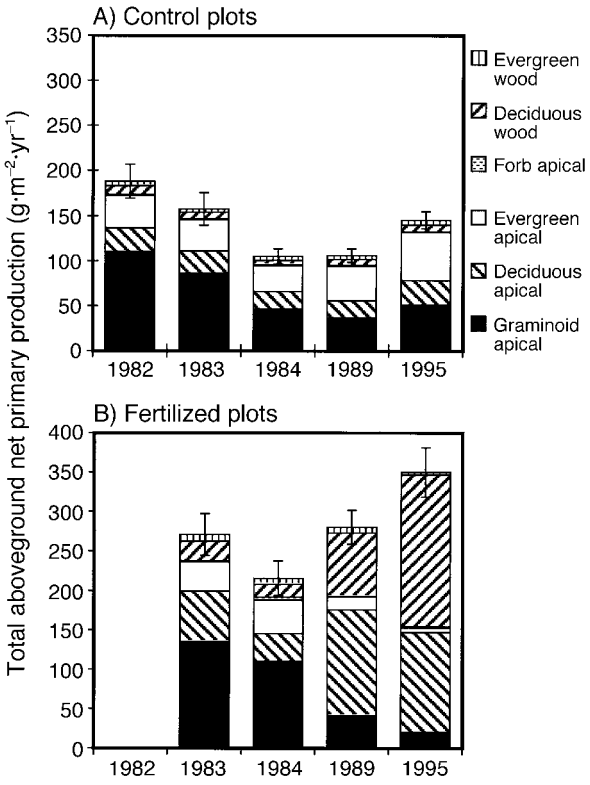

FIG. 4. Total aboveground net primary production, ANPP (mean ± 1 SE), in (A) control and (B) fertilized plots, 1982–1995. The lower segments of each bar indicate the apical growth component of ANPP in the four major growth forms, with forb biomass included but always too small to be seen at this scale. Upper segments indicate secondary growth by deciduous and evergreen shrubs.

control plots (Table 6; $P < 0.001$). This overall increase was consistent with the 2.5-fold increase in vascular biomass and the 2.4-fold increase in ANPP (Table 4), so the weighted-average N concentration in aboveground biomass was similar in both treatments at 1.2% (slightly but not significantly lower in the fertilized treatment). This relatively constant overall N concentration, however, was the result of compensatory changes both in N concentration within growth forms and in the relative abundance of growth forms that differed in N concentration. Particularly important were relatively large increases in N concentration in graminoid and evergreen species in fertilized plots, balanced against relatively small decreases in overall N concentration of deciduous species (data for individual species are not shown except for *Betula*; Table 7).

Because *Betula* was so strongly dominant in the fertilized plots, changes in the proportional allocation of its biomass and N content were particularly important in determining overall changes in N mass and concentration. In *Betula* alone, both biomass and N concentration increased with fertilization in all tissues (Table 7). The mass of old aboveground stems increased 12.5-fold, however, whereas the mass of leaves increased only fivefold (both $P < 0.001$). Increases in N concentration were much smaller, not significantly so in stems (from 0.8% N to 0.89% N) and by ~20% in leaves (from 2.1% N to 2.6% N; $P < 0.05$). Thus, changes in the relative masses of tissues that differed in N concentration were more important than changes in concentration within tissues. Because stem mass increased more than twice as much as leaf mass did, the overall weighted-average aboveground N concentration was unchanged in fertilized *Betula*, at 1.1% (Table 7). Because *Betula* was the dominant plant in the fertilized plots, the weighted-average aboveground N concentration for the vegetation as a whole did not change (Table 6).

The mass of N in leaves, on the other hand, was only 30% higher in fertilized relative to control plots in 1995 (Table 6; $P < 0.007$), a much smaller increase than the 2.4-fold increase in total aboveground N mass and in the opposite direction from the 21% *decrease* in total leaf mass (Table 5). This increase in leaf N mass was the result of increases in N concentration in all three major growth forms, combined with an increase in relative abundance of deciduous leaves (mainly *Betula*) that had the highest leaf N concentrations. Thus, increases in average leaf N concentration more than compensated for decreases in leaf mass, mainly because of the change in species composition.

The leaf area per unit N mass (nitrogen specific leaf area, or NSLA) also was changed by the fertilizer treatment in 1995. Overall, there was a 54% increase in vascular NSLA in the fertilized plots (Table 6), due principally to the strong dominance of *Betula* in this treatment. Within species and growth forms, NSLA sometimes increased and sometimes decreased with fertilization, depending on the relative magnitudes of the increases in leaf N concentration (which tended to decrease NSLA) vs. the increases in SLA (which tended to increase NSLA if N concentration remained the same or decreased). In *Betula* and in deciduous species as a group, NSLA increased by 21% in fertilized plots because the increases in N concentration (22%) were smaller than the increases in SLA (38%). In the graminoids and the evergreens, NSLA declined with fertilization because the increases in N concentration (51% and 60%, respectively) were greater than the increases in SLA (16% and 32%).

Production vs. biomass, leaf mass, leaf area, and leaf N

Production–biomass relationships in control plots were remarkably consistent among the five harvests from 1982 to 1995 (Fig. 5A; $r^2 = 0.97$, $P < 0.001$). The range in production:biomass ratio in control plots was 0.4:1 to 0.5:1 among the five years when the control plots were harvested. Assuming relatively steady-state conditions, this would indicate an aboveground biomass turnover time of ~2–2.5 yr in control plots.

TABLE 5. Leaf area, leaf mass, and specific leaf area in control and fertilized plots in the 1995 harvest (values are means ± 1 SE).

Growth form and species	Tissue	Leaf area (m^2 leaf/m^2 ground)		Leaf mass (g leaf/m^2 ground)	
		Control	N + P fert.	Control	N + P fert.
Graminoid					
E. vaginatum	blade	0.218 ± 0.009	0.054 ± 0.027	27.06 ± 5.48	5.43 ± 2.50
Carex bigelowii	blade	0.022 ± 0.002	0.019 ± 0.007	2.57 ± 0.89	2.27 ± 1.04
Other graminoid	blade	0.005 ± 0.001	0.089 ± 0.060	0.78 ± 0.47	8.53 ± 5.50
Deciduous					
Betula nana	new	0.194 ± 0.007	1.321 ± 0.151	14.46 ± 2.43	74.83 ± 7.30
Salix spp.	new	0.014 ± 0.002	0.003 ± 0.002	1.46 ± 1.01	0.23 ± 0.17
Vaccinium uliginosum	new	n.d.	0.000 ± 0.000	0.01 ± 0.01	0.00 ± 0.00
Rubus chaemamorus	new	0.026 ± 0.002	0.403 ± 0.078	2.38 ± 0.81	17.94 ± 3.62
Other deciduous	new	0.030 ± 0.007	0.000 ± 0.000	2.79 ± 2.79	0.00 ± 0.00
Evergreen					
Ledum palustre	new	0.096 ± 0.003	0.025 ± 0.010	21.83 ± 2.51	4.39 ± 1.91
	old	0.084 ± 0.003	0.020 ± 0.007	20.92 ± 3.17	3.79 ± 1.40
Vaccinium vitis-idaea	new	0.113 ± 0.003	0.001 ± 0.001	19.62 ± 2.25	0.13 ± 0.07
	old	0.139 ± 0.004	0.003 ± 0.002	31.30 ± 4.64	0.49 ± 0.28
Other evergreen	new	0.011 ± 0.001	n.d.	1.82 ± 0.57	0.01 ± 0.01
	old	0.013 ± 0.001	n.d.	3.60 ± 1.26	0.10 ± 0.10
Forbs	new	0.002 ± 0.000	n.d.	0.49 ± 0.20	1.35 ± 1.05
Totals					
Graminoid	blade	0.246 ± 0.010	0.163 ± 0.062	30.41 ± 5.63	16.23 ± 5.76
Deciduous	new	0.263 ± 0.009	1.728 ± 0.185	21.10 ± 3.40	93.01 ± 8.70
Evergreen	all	0.455 ± 0.009	0.049 ± 0.019	99.08 ± 9.61	8.90 ± 3.47
Total vascular	all	0.966 ± 0.014	1.940 ± 0.159	151.08 ± 11.10	119.48 ± 7.68

Notes: In some cases where leaf mass was very small or zero, accurate leaf areas could not be determined, and specific leaf areas could not be calculated (indicated as n.d., not determined). Because these instances accounted for very small portions of total leaf areas and weighted-average specific leaf areas, the missing cells were ignored in the total and overall calculations.

† $n = 1$.

The production:biomass ratio was slightly greater in years when both production and biomass were high, and lower in years when both production and biomass were low, as might be expected if species with high relative growth rates and high biomass turnover were relatively more important in years of high overall biomass and productivity (e.g., Chapin and Shaver 1985, Hobbie 1996).

Production–biomass relationships were changed greatly by the fertilizer treatment, and continued to change from 1983 to 1995 (Fig. 5A). In the early harvests of the fertilizer treatment (1983 and 1984), both production and biomass increased in fertilized plots relative to controls, but production increased relatively more. After 1984, however, biomass continued to increase in the fertilized plots, but production increased more slowly. As a result, the production:biomass ratio declined from a high of 0.66 in 1983, to 0.61 in 1984, 0.54 in 1989, and 0.41 in 1995. This would indicate a minimum biomass turnover time of 2.4 yr in fertilized plots in 1995, about the same as in control plots where production:biomass ratio was 0.47 in 1995 (turnover time 2.1 yr). The actual biomass turnover time in fertilized plots was probably longer, though, because the fertilized plots were not in steady state and were still accumulating biomass. Production per unit aboveground N mass was also similar in the two treatments in 1995 (Table 8).

The changes in production:biomass relationships in fertilized plots after 1984 were due largely to the increased dominance of *Betula,* with its large woody stem mass. In 1989 and 1995, the apical growth component of primary production actually declined in fertilized plots ($P < 0.04$), as secondary growth and total production both increased ($P < 0.0001$ and $P < 0.02$, respectively; Fig. 4B). Total biomass continued to increase as a result of fertilization ($P < 0.0001$) but most of these increases were in relatively inactive woody stem mass (Table 4).

Relationships between production and leaf mass were also changed dramatically by the fertilizer treatment, but again the changes took at least nine years to develop and were due mainly to the increasing dominance of *Betula.* Before 1989, in fertilized plots the production per unit leaf mass was close to the predicted relationship obtained by regression of control plot data ($r^2 = 0.99$, $P < 0.001$; Fig. 5B). Where there was a deviation from the predicted value (as in 1983), it could be explained largely as the result of fertilizer-caused, within-species increases in SLA (Table 5). By 1995, however, *Betula* (with its much higher SLA) was so strongly dominant in the fertilized plots that community production per unit leaf mass was more than twice what would be predicted by extrapolation from control plot harvests.

Aboveground production was also tightly correlated

TABLE 5. Extended.

Specific leaf area (cm^2 leaf/g leaf)	
Control	N + P fert.
81.77 ± 2.07	93.46 ± 5.25
83.04 ± 5.38	164.90 ± 67.94
70.23 ± 11.02	91.81 ± 13.48
136.91 ± 3.59	173.51 ± 5.90
98.73 ± 23.69	144.13 ± 9.50
n.d.	n.d.
130.22 ± 10.46	264.05 ± 56.50
107.35†	n.d.
43.63 ± 2.21	64.35 ± 5.10
41.03 ± 1.01	58.82 ± 5.70
59.40 ± 1.69	122.87 ± 18.62
45.99 ± 1.35	84.15 ± 14.45
97.67 ± 51.57	n.d.
41.82 ± 3.45	n.d.
88.16 ± 19.59	n.d.
81.80 ± 2.06	94.53 ± 6.10
131.24 ± 4.06	181.79 ± 5.54
46.80 ± 1.02	62.01 ± 5.11
65.28 ± 2.02	162.22 ± 7.74

TABLE 7. Aboveground biomass and N concentration (mean ± 1 SE) in *Betula nana* in control and fertilized plots in 1995.

Productivity and N status of *Betula* tissues†	Control	Fertilized
Biomass (g/m^2)		
Leaves	14.46 ± 2.43	74.83 ± 7.30
New stem	4.27 ± 0.87	25.29 ± 2.86
Old stem	49.87 ± 9.12	624.44 ± 86.95
Inflorescence	0.22 ± 0.10	6.11 ± 1.68
Overall	68.83 ± 12.22	730.68 ± 94.29
N concentration‡ (%)		
Leaves	2.11 ± 0.01	2.58 ± 0.04
New stem	1.73 ± 0.06	1.94 ± 0.05
Old stem	0.80 ± 0.03	0.89 ± 0.04
Inflorescence	1.85 ± 0.12	2.03 ± 0.03
Overall§	1.14 ± 0.07	1.11 ± 0.10

† Leaves, new stems, and inflorescences are the product of current year's apical growth. Old stems increase in mass each year through secondary growth and by addition of the previous year's new stems to the old stem category.

‡ N concentrations are expressed as percentages of dry mass ($n = 4$). One sample of each biomass category was analyzed for N from each block (after weighing, samples from the five quadrats per block were lumped for analysis).

§ The weighted average of all aboveground biomass ($n = 4$), with individual values for each block calculated by multiplying N concentration of each category by its corresponding mass to produce an estimate of N mass, then finding the sum of the N masses, and finally dividing by total mass.

with leaf area in control plots ($r^2 = 0.96$, $P < 0.001$), but was not correlated with leaf area in fertilized plots (Fig. 5C). Furthermore, there was no trend over time in the relationship between production and leaf area in the fertilized plots that might be related to the shift in species composition. Although leaf area was always greater in fertilized than in control plots, leaf area in fertilized plots was lowest in 1984, highest in 1989, and intermediate in 1983 and 1995. On the whole, this pattern is consistent with the interpretation that some other factor, probably light, became limiting on the fertilized plots almost immediately after the beginning of the treatments. The transition occurred above an average leaf area of ~1.50 m^2 leaf/m^2 ground, which was not reached by unfertilized tussock tundra in any of the five years it was harvested (Fig. 5C).

By the time of the 1995 harvest, *Betula* in particular, and the deciduous species as a group, were much more productive in fertilized plots by most of these relative measures of leaf ''efficiency'' (ANPP per unit leaf mass, per unit leaf area, and per unit leaf N mass) than were any of the graminoid or evergreen species (Table 8). This greater relative productivity of *Betula* in the

TABLE 6. Nitrogen mass and nitrogen concentration in aboveground biomass and in leaves (values are means ± 1 SE), and nitrogen-specific leaf area (NSLA) in control and fertilized plots in the 1995 harvest.

N source and growth form	N mass† (g/m^2)		N concentration‡ (%)		NSLA§ (cm^2/g N)	
	Control	Fertilized	Control	Fertilized	Control	Fertilized
Total aboveground N						
Graminoid	0.773 ± 0.143	0.52 ± 0.23	1.50	2.46		
Deciduous	1.019 ± 0.109	8.58 ± 0.78	1.25	1.16		
Evergreen	2.12 ± 0.29	0.42 ± 0.23	1.16	1.49		
Total vascular	3.92 ± 0.26	9.57 ± 0.90	1.24	1.21		
Leaf N						
Graminoid	0.54 ± 0.09	0.44 ± 0.19	1.79	2.56	4509	3706
Deciduous	0.45 ± 0.03	2.45 ± 0.27	2.14	2.64	5821	7050
Evergreen	1.40 ± 0.20	0.20 ± 0.10	1.41	2.14	3244	2451
Total vascular	2.41 ± 0.17	3.14 ± 0.21	1.60	2.62	4005	6187

† Nitrogen mass was calculated by multiplying the N concentrations of individual species and tissue types by their corresponding biomass values and summing the products.

‡ Nitrogen concentration is a weighted average, calculated by dividing the mean N mass by the corresponding mean biomass values from Tables 4 or 5.

§ NSLA was calculated by dividing mean leaf area (Table 5) by mean leaf N mass.

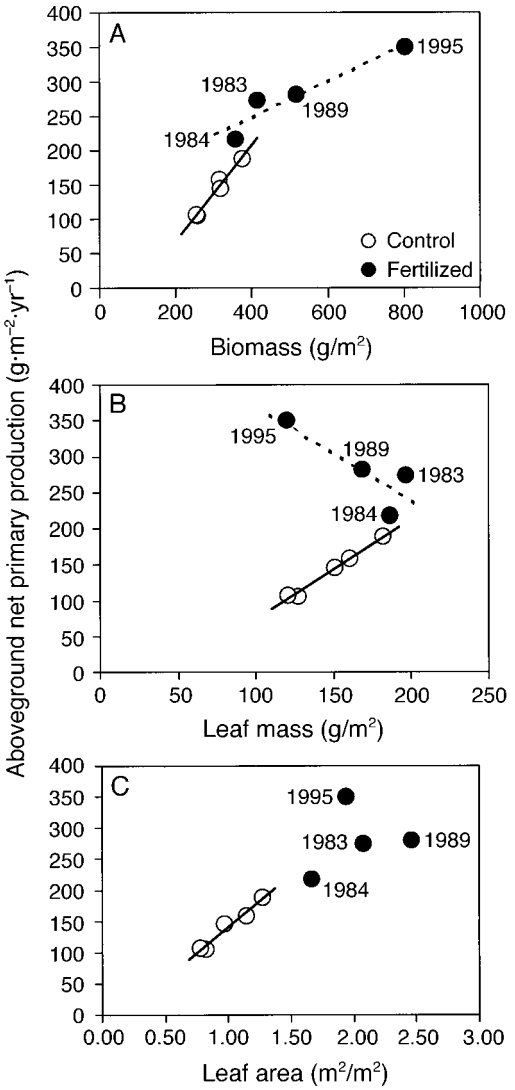

FIG. 5. Relationships of vascular aboveground net primary production (ANPP) to (A) aboveground biomass, (B) total vascular leaf mass, and (C) total vascular leaf area in control and fertilized plots, 1982–1995. Data points are the mean values for ANPP, biomass, leaf mass, and leaf area for each treatment and year. Leaf areas for 1995 are taken from Table 5; for 1982–1989, leaf areas were estimated by multiplying leaf mass for each species, treatment, and year by their respective 1995 specific leaf areas (Table 5).

fertilized plots may explain its dominance there. Importantly, *Betula* and the deciduous species as a group were *not* the most productive, by any of these three measures, in the control plots in 1995, suggesting that one of the reasons for the higher diversity in unfertilized vegetation may be that no species or growth form has a particularly strong advantage in production ''efficiency'' there. In control plots, the graminoids had the highest relative productivity by almost all measures. Further adjustment of the measures in Table 8 to account for the longer leaf life-span of evergreens (e.g., by multiplying ANPP per unit leaf mass times leaf longevity; Johnson and Tieszen 1976, Shaver 1983) would increase the apparent leaf ''efficiency'' of evergreens, particularly in control plots. Further adjustments, however, are unlikely to change the apparently much greater leaf ''efficiency'' of *Betula* in the fertilized plots, especially with respect to leaf N mass in this strongly N-limited ecosystem (Shaver et al. 1986, Chapin et al. 1995).

Vegetation and canopy structure

The structure of aboveground biomass and the display of leaf area were very different in control and fertilized plots in 1995, as indicated by the results of the point-frame sampling (Fig. 6). Each pin hit in the fertilized plots was associated with much higher biomass or much greater leaf area than in control plots, with little overlap between the two groups of data points in either case. Separate regressions of data by treatment were highly significant (all $P < 0.001$; $r^2 = 0.72$ and 0.47 for control and fertilized biomass, respectively; $r^2 = 0.69$ and 0.75 for control and fertilized leaf area, respectively), as were overall regressions

TABLE 8. Aboveground net primary production (ANPP) per unit aboveground biomass, N mass, leaf mass, leaf area, and leaf nitrogen for the 1995 harvest of control and fertilized plots at Toolik Lake.

ANPP measures for growth forms and *Betula*	Control	Fertilized
ANPP/aboveground biomass ($g \cdot g^{-1} \cdot yr^{-1}$)		
Graminoid	1.00	1.00
Deciduous	0.42	0.39
Evergreen	0.35	0.28
Total vascular	0.47	0.41
Betula	0.37	0.41
ANPP/aboveground N mass ($g \cdot g^{-1} \cdot yr^{-1}$)		
Graminoid	66.40	39.73
Deciduous	33.93	37.22
Evergreen	27.83	21.74
Total vascular	37.09	36.56
Betula	32.61	37.16
ANPP/leaf mass ($g \cdot g^{-1}$ leaf$\cdot yr^{-1}$)		
Graminoid	1.69	1.24
Deciduous	1.63	3.18
Evergreen	0.63	0.93
Total vascular	0.99	2.73
Betula	1.78	3.97
ANPP/leaf area ($g \cdot m^{-2}$ leaf$\cdot yr^{-1}$)		
Graminoid	209.02	122.95
Deciduous	130.52	171.31
Evergreen	137.98	168.12
Total vascular	154.26	167.86
Betula	132.83	225.11
ANPP/leaf N mass ($g \cdot g^{-1}$ N$\cdot yr^{-1}$)		
Graminoid	94.26	45.57
Deciduous	75.98	120.78
Evergreen	44.77	41.21
Total vascular	61.78	103.85
Betula	84.71	154.22

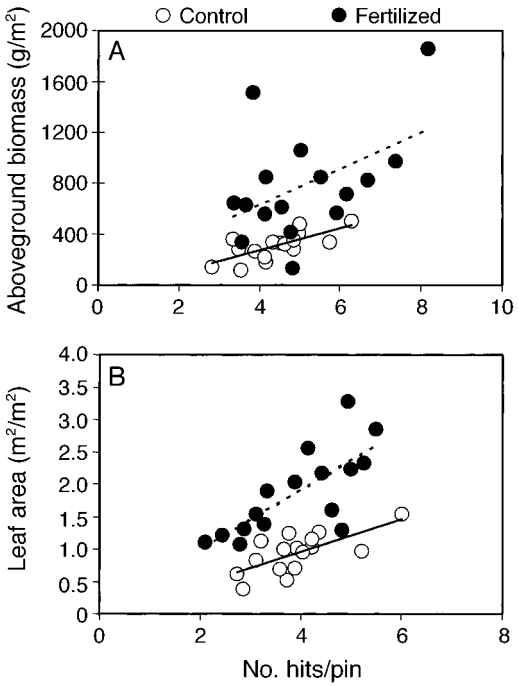

FIG. 6. (A) Aboveground vascular plant biomass in relation to the total number of hits per point-frame pin in control and fertilized plots in the 1995 harvest. (B) Vascular leaf area in relation to number of leaf hits per pin. Data points represent individual quadrats of control or fertilized treatments (n = 16 of each treatment). Solid lines were calculated by linear regression of control data points, dashed lines by regression of fertilized data points. Statistics for the overall regression (n = 32) are given in Table 9.

(i.e., combining the two treatments; Table 9), but the overall regressions had little predictive value ($r^2 = 0.29$ and 0.27, respectively). Analyses of covariance (SYSTAT 1998, version 8.0) showed that the regression slopes for each treatment were not significantly different for either biomass (Fig. 6A) or leaf area (Fig. 6B), but the adjusted means in both cases differed significantly (both $P < 0.001$).

Examination of the point-frame results for individual growth forms and species reveals the cause of the treatment differences in vegetation structure and leaf display (Table 9, Figs. 7 and 8). That is, the overall treatment differences in Fig. 6A and B were caused entirely by changes in the relative abundances of species and growth forms with different biomass structure and leaf display. For the three major growth forms, the slopes of separate regressions for data from control vs. fertilized treatments (Figs. 7 and 8) did not differ significantly except for aboveground biomass in graminoids (Fig. 7A; the interaction between treatment and number of hits was significant at $P < 0.001$). The difference in slopes for graminoid biomass was due to a single outlying data point from the fertilized treatment. When this outlier was deleted, adjusted mean values for biomass or leaf area in Figs. 7 and 8 also did not differ significantly in any comparison. Thus, there was no indication of a change in biomass structure or leaf display within species as a result of fertilizer treatment. Rather, it was the differences in species composition between control and fertilized treatments that caused the overall treatment differences in Fig. 6, due to the different relationships for each species and growth form between pin hits and biomass or leaf area (Table 9).

Species and growth form differences in the point-frame results reflected fundamental differences in plant architecture. Graminoids had the least biomass per pin hit, and thus the shallowest slopes for this relationship (Table 9), because their tissues are all nonwoody, and thus less dense, than the more woody deciduous species or the sclerophyllous evergreen species. Graminoids also tended to be more clumped in their distribution, with groups of leaves attached to individual tillers and groups of tillers growing in tussocks, so individual pins that happened to pass through a graminoid canopy were more likely to have multiple hits. The dominant evergreen, *Ledum palustre*, had the smallest leaf area per pin hit and the shallowest regression slope for this relationship (Table 9), because it had narrow, needle-like leaves with low SLA (high mass per unit area). Deciduous species (mainly *Betula*) had the steepest regression slopes for both biomass and leaf area (Table 9) because of their woodiness and their thin, broad, more horizontally oriented leaves. Because these relationships had different slopes for each functional type, and the relative abundance of each functional type varied among quadrats (especially in control plots), the accuracy of predictions of biomass or leaf area based on hits in whole vegetation will be less accurate than predictions calculated as the sum of predictions for individual functional types.

DISCUSSION

Long-term change in control plots

Long-term change and variation in control plots provide an important context for interpretation of the responses to fertilizer that we observed. It is particularly noteworthy that the aboveground production of control plots was slightly *more* variable among years (CV = 25%) than was the production of fertilized plots (CV = 19%), despite large increases in biomass on the fertilized plots. The most likely explanation for this result is that the fertilizer treatment quickly eliminated any nutrient limitation; hence, from at least 1983 to 1995, the fertilized community's production was responding principally to annual variation in light and temperature, not nutrient supply. The greater annual variation in production in control plots probably reflects the additional effect of annual variation in nutrient supply, either as current uptake or as storage and recycling from previous years' uptake.

Individual species were more variable in their annual

TABLE 9. Linear regression parameters for relationships between (A) total aboveground biomass and the number of point-frame hits on total aboveground biomass (sum of all leaf, stem, and inflorescence hits), and (B) between leaf area and hits on leaves only.

Biomass and leaf area for growth forms and species	Slope			Intercept			Overall regression	
	Value	1 SE	*P*	Value	1 SE	*P*	r^2	*P*
A) Aboveground biomass								
Graminoid	0.023	0.003	0.000	0.002	0.221	0.99	0.73	0.000
Deciduous	0.126	0.011	0.000	−2.11	2.11	0.34	0.81	0.000
Evergreen	0.043	0.004	0.000	−0.211	0.496	0.67	0.81	0.000
Total vascular	0.108	0.031	0.001	−11.1	9.63	0.26	0.29	0.001
Eriophorum vaginatum	0.033	0.003	0.000	−0.330	0.146	0.03	0.85	0.000
Betula nana	0.136	0.010	0.000	−1.294	1.832	0.49	0.85	0.000
Ledum palustre	0.040	0.005	0.000	−0.036	0.382	0.92	0.70	0.000
Vaccinium vitis-idaea	0.048	0.002	0.000	−0.030	0.114	0.80	0.93	0.000
B) Leaf area								
Graminoid	1.60	0.09	0.000	−14.4	7.7	0.07	0.91	0.000
Deciduous	3.76	0.15	0.000	−21.1	20.5	0.31	0.96	0.000
Evergreen	1.22	0.10	0.000	−3.2	11.4	0.78	0.82	0.000
Total vascular	2.37	0.71	0.002	−31.9	182.9	0.86	0.27	0.002
Eriophorum vaginatum	1.67	0.10	0.000	−16.0	5.5	0.01	0.91	0.000
Betula nana	3.40	0.12	0.000	−4.8	14.7	0.74	0.96	0.000
Ledum palustre	0.77	0.09	0.000	4.2	6.2	0.50	0.70	0.000
Vaccinium vitis-idaea	1.88	0.10	0.000	1.6	3.9	0.68	0.93	0.000

Notes: In these regressions, aboveground biomass or leaf area is predicted by number of hits according to the formula: Mass (g/quadrat) or leaf area (cm^2/quadrat) = slope × (no. hits/quadrat) + intercept. Quadrat size was 400 cm^2 (20 × 20 cm), so conversion of biomass to g/m^2 requires multiplying by 25, and conversion of leaf area to m^2/m^2 requires multiplying by 2.5×10^{-3}. The prediction is also a function of the number of pins per quadrat (64 in this case) and pin diameter (5 mm). In all regressions, all quadrats were treated as independent samples, so the sample size was 32 (16 control quadrats plus 16 fertilized quadrats).

production and biomass at Toolik Lake than was the whole community, as we found previously at Eagle Creek, in interior Alaska (Chapin and Shaver 1985). At Toolik Lake, however, all four of the most abundant species in the control plots declined simultaneously in aboveground production and biomass following the 1982 harvest; reached a minimum in 1983, 1984, or 1989; and then increased together from 1989 to 1995. Thus, at Toolik Lake there was relatively little compensation at the community level that results from one species having an ''up'' year while others had ''down'' years, such as we saw at Eagle Creek. Overall, between 1982 and 1995 at Toolik Lake, the relative abundance of the two dominant evergreens, *Ledum palustre* and *Vaccinium vitis-idaea*, increased in the control plots, while *Eriophorum vaginatum* declined from first to fourth in abundance and *Betula nana* remained in third place. Moss and lichen biomass also declined. We have no basis for knowing whether these trends will continue or whether the results of our five harvests over 14 yr have documented a typical long-term pattern of fluctuation in species composition. It is quite possible that the changes we observed at Toolik Lake from 1982 to 1995 (and the relative stability of productivity at Eagle Creek from 1968 to 1981) are related to the regional warming trend that began in Alaska in the mid-1980s (Chapman and Walsh 1993, Serreze et al. 2000).

Long-term change in fertilized plots

Even after 15 yr of treatment, the fertilized plots had not reached a new steady state. Between 1989 and 1995, aboveground vascular biomass in fertilized plots increased by >50% and productivity by 25%, and there were large changes in overall biomass allocation, biomass turnover, leaf production, and leaf area–mass relationships. Dwarf birch, *Betula nana*, more than doubled its biomass in the six years from 1989 to 1995, while almost all other species declined in abundance and three species were lost entirely. In comparison, over the previous 6-yr period (1983–1989), aboveground biomass of fertilized plots increased by only 24% and there was no significant change in aboveground production (Chapin et al. 1995). Although birch biomass tripled from 1983 to 1989, the amount of the increase (225 g/m^2) was less than the increase from 1989 to 1995 (370 g/m^2). It is not clear how long these trends might continue. If anything, however, the rate of biomass accumulation in response to fertilizer appears to have *increased* over time.

Continued long-term changes in fertilized plots could have three main causes. The first of these is uncontrolled, background change in the environment, as revealed in harvest-to-harvest variation in control plots. For example, the fact that the lowest production and biomass in control plots were observed in 1984

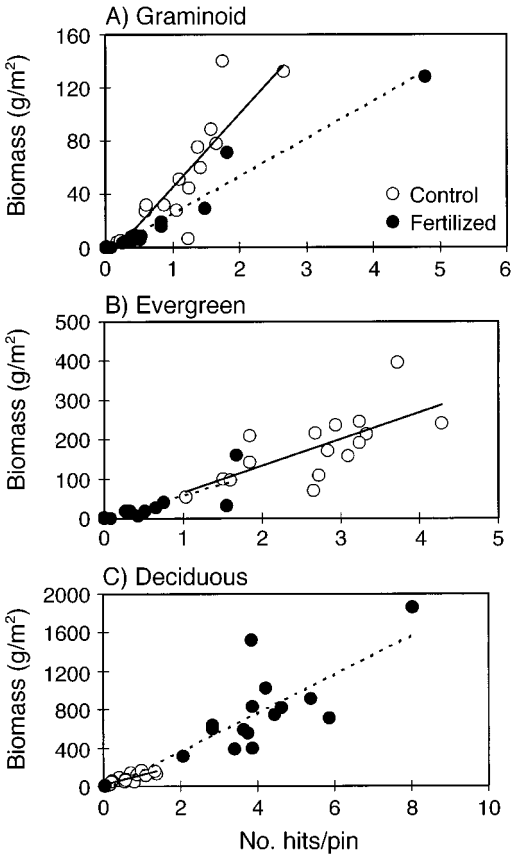

FIG. 7. Aboveground biomass of (A) graminoid, (B) evergreen, or (C) deciduous species in relation to the total number of hits per point-frame pin in control and fertilized plots in the 1995 harvest. Data points represent individual quadrats of control or fertilized treatments (n = 16 of each treatment). Solid lines were calculated by linear regression of control data points, dashed lines by regression of fertilized data points. Statistics for the overall regression (n = 32) are given in Table 8. Note that both vertical and horizontal scales differ among the three graphs.

and 1989 indicates relatively poor growing conditions in those years, which, at least in part, might explain the relatively small production and biomass increases in fertilized plots from 1983 to 1989. The second cause of long-term change in fertilized plots is continued increases in annual nutrient uptake by the vegetation as biomass increases incrementally from year to year. In other words, nutrient uptake capacity (and potential productivity) may be limited in the first years simply by the small initial size of the plants. It may take many years for biomass and production to come into equilibrium with a greatly increased annual nutrient supply. Finally, changes in species composition and replacement of large, old, individual plants may affect both the rate of change over many years and the final biomass and production. The present study provides evidence that this third category of change is also of major importance in regulating long-term ecosystem-level change.

Species effects

Changes in species composition in fertilized plots had different effects on production and biomass before and after 1989. In the years before 1989, species other than *Betula* accounted for the majority of the biomass, and nearly all species initially increased their annual growth in response to fertilizer addition (Shaver and Chapin 1980, Chapin and Shaver 1985, 1996), leading to the large increase in production relative to control plots in 1983, for example. Between 1983 and 1989, however, only *Betula*, *Rubus*, and ''other graminoids'' (mainly grasses) continued to increase in abundance on

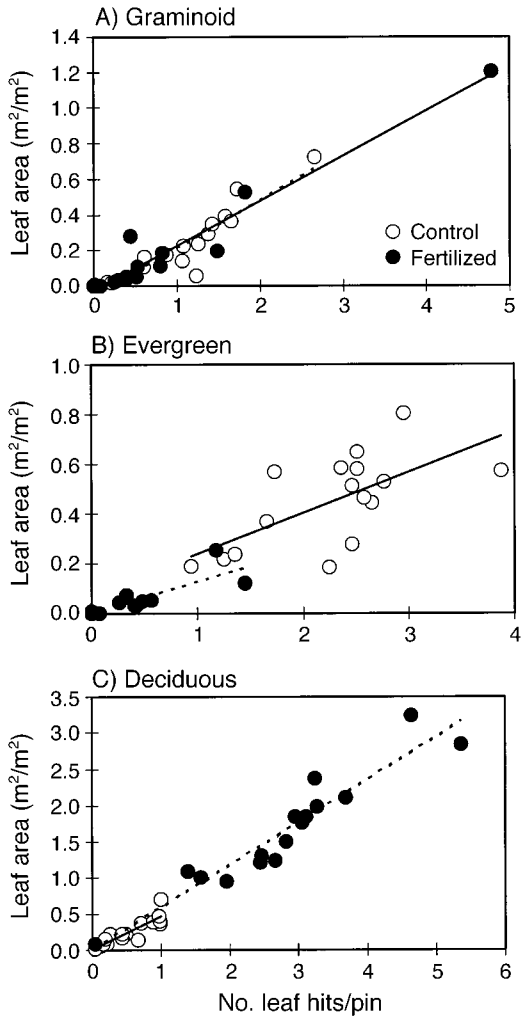

FIG. 8. Leaf area of (A) graminoid, (B) evergreen, or (C) deciduous species in relation to the total number of leaf hits per point-frame pin in control and fertilized plots in the 1995 harvest. Data points represent individual quadrats of control or fertilized treatments (n = 16 of each treatment). Solid lines were calculated by linear regression of control data points, dashed lines by regression of fertilized data points. Statistics for the overall regression (n = 32) are given in Table 8. Note that both vertical and horizontal scales differ among the three graphs.

the fertilized plots, while others declined. This large loss due to mortality of formerly abundant species was more than compensated by increases in *Betula* alone, but the replacement process still introduced a lag time of several years before production and biomass in fertilized plots fully reflected the new species composition.

After 1989, the fertilized vegetation was so strongly dominated by *Betula* that overall production, biomass, and turnover characteristics were determined principally by this one species. The characteristics of *Betula* that were most important in allowing it to become dominant were (1) its very high SLA and NSLA relative to other species in the vegetation, particularly in fertilized plots; and (2) its high proportional allocation to secondary growth (wood production). These two characteristics are related, in that large amounts of wood production are possible, in part, because leaf area production costs are so low; i.e., resources not used in leaf production can be reallocated to other purposes including wood production. Because wood has a high C:N ratio (low N concentration), relatively large amounts of wood can be produced per unit N, the most limiting element in this ecosystem. From previous work on the same plots (Chapin and Shaver 1996), we also know that *Betula's* photosynthetic rate per unit leaf mass is much greater in both fertilized and control plots (1.2- to 10-fold greater) than in any other dominant species, although when the rates are expressed per unit leaf area (dividing the rate per unit mass by SLA), the rates for all dominant species are similar (Bret-Harte et al. 2001).

Another advantageous trait is that fertilized *Betula* can produce new meristems more rapidly than any other initially dominant species or other common but less abundant species like *Salix pulchra.* Thus *Betula* can grow more rapidly when fertilized because it can rapidly add both new leaf area and new sinks for additional resources (Bret-Harte et al. 2001). Rapid branch production by fertilized *Betula* leads to rapid increases in numbers of stems. The large increases in overall wood production that we observed were due to increased stem numbers as well as increased secondary growth of individual stem segments (M. S. Bret-Harte and G. R. Shaver, *unpublished data*).

An important consequence of dominance by *Betula* was that the overall concentration of N (the element most limiting to plant growth) in aboveground biomass was essentially the same in fertilized plots (1.21%) as in control plots (1.24%). This occurred because the fertilized *Betula* produced a relatively small amount of high-N leaf mass and a large amount of low-N stem mass. Overall, aboveground N concentrations in *Betula* alone were 1.14% in controls and 1.11% in fertilized plots, because stem mass accounted for an even higher proportion of its total aboveground mass in fertilized plots than in controls. Because of this increased allocation to stem mass, production per unit biomass and per unit N mass increased in *Betula* due to fertilization, whereas they decreased or were unchanged in the other plant forms. Thus, dominance by *Betula* in fertilized plots led to a greater increase in production and biomass than would have occurred if species composition had not changed.

A second consequence of these growth characteristics is that, under fertilized conditions, *Betula* grew taller as well as faster than other species, thus dominating the upper canopy. *Betula* grew taller because it produced thicker, stronger woody stems, and because its more rapid branching took place relatively high up on those stems (Bret-Harte et al. 2001). By 1989, average canopy height in the fertilized plots was 38 cm vs. 21 cm in the controls (Chapin and Shaver 1996). The taller canopy with greater leaf area reduced light penetration to the soil surface to $<15\%$ of control plots (Bret-Harte et al. 2001), thus greatly reducing light available to subcanopy species. Growth of mosses and other low-growing species was further inhibited by the accumulation of 2–5 cm of *Betula* leaf litter over much of the soil surface. The reduced light penetration to the surface and increased litter accumulation at the surface were sufficient to reduce the annual depth of soil thaw in 1989 from 38.3 cm to 31.7 cm (Chapin et al. 1995). In the absence of annual fertilizer addition, these changes in soil thaw would be expected to reduce N mineralization and thus N availability, limiting the large increases in productivity, aboveground biomass, and leaf area that we observed.

A final consequence of the dominance by *Betula* in fertilized plots, not investigated in this study, is the relatively slow rate of decomposition of *Betula* litter relative to other species. Both leaf and stem litter of *Betula* decompose more slowly than leaves and stems of other species, and *Betula* litter includes a higher proportion of stems, which are particularly slow to decompose (Hobbie 1996). The increased dominance of *Betula* in fertilized plots should lead to a slower overall turnover of C and N in litter, although we might expect the fertilizer treatment directly to increase litter turnover by increasing litter N content, and thus its decomposability, within species.

Vegetation and canopy structure

Within species and plant functional types, the fertilizer treatment apparently had no effect on size–structure relationships or canopy allometry, as shown by the point-frame results. These data indicate a constant, linear relationship between pin hits and biomass or leaf area within each growth form across treatments. Thus, although the fertilizer did have a major effect on both biomass and leaf area for all species, the structure of the biomass and the display of leaf area followed the same allometric rules in both treatments. This is important because, for example, it suggests that the increased proportional allocation to woody stems in *Betula* in the fertilized treatment is mainly a simple func-

tion of plant size and is not an additional treatment effect on allocation.

Because there were no treatment effects on underlying size–structure relationships within species or functional types, changes in overall biomass structure and canopy display in the fertilized treatment were entirely attributable to the change in species and functional type composition, as the community changed from a mix of graminoid, deciduous, and evergreen species to one strongly dominated by deciduous species only. The physical structure of vegetation is particularly important in the arctic, because it has a major impact on surface temperature and energy and water balance (e.g., McFadden et al. 1998). Our results indicate that, at any given biomass or leaf area, it is essential to identify species or at least functional types in order to predict surface characteristics and fluxes accurately.

Conclusions and future predictions

Changes in species composition in the Toolik Lake fertilizer experiment have a distinct, detectable impact on aboveground production, aboveground biomass, element cycling, and vegetation structure. This impact is qualitatively different from, and in addition to, the effect of increased nutrient availability through 15 yr of fertilizer addition. Our results thus support and extend the growing body of evidence that species composition is an important control over ecosystem biogeochemistry (e.g., Berendse and Jonasson 1992, Hobbie 1995, Wedin and Tilman 1996, Chapin et al. 1997, Jonasson and Shaver 1999, van Oene et al. 1999). The principal contribution of the present study is its detailed demonstration of the importance of species differences in SLA and NSLA, and in the allocation of C and N between leaf and stem tissues. These characteristics are major determinants of ''nutrient use efficiency'' (Berendse and Aerts 1987, Aerts and van der Peijl 1993, Aerts and Caluwe 1994) and ''nutrient productivity'' (Ågren 1985, Ågren et al. 1999) at both the species and the ecosystem level.

Our most surprising result is that, because of the dominance of *Betula* in the fertilized plots, the fertilized vegetation actually accumulates *more* aboveground biomass per unit N, and it produces *more* per unit leaf N, than the unfertilized vegetation. Nitrogen is a strongly limiting element in unfertilized vegetation at this site (Shaver et al. 1986). This raises the question, ''Why isn't *Betula* more dominant in control plots?'' Intuitively, we would expect the species that uses the most limiting resource most effectively to be dominant (Aerts and van der Peijl 1993, Herbert et al. 1999). The explanation may be related to the low total N availability in control plots, which might prevent *Betula* from producing enough high-N leaf mass to support the C costs of producing and maintaining a large woody stem mass. In other words, nutrient use and allocation are not the only important factors that determine species composition in unfertilized tundra. Explanation of the changes that we observed in Alaska is complicated further by the very different responses to fertilizer addition at Abisko, Sweden, where *Betula nana* is relatively *unresponsive* to fertilizer addition (Graglia et al. 1997) and *does not* become dominant after 5 or 10 yr of fertilization (Jonasson et al. 1999; S. Jonasson, *personal communication*). The question requires additional research to provide a clear answer.

Finally, we must remember that the Toolik Lake fertilized plots are still changing in species composition, in production and biomass, and in canopy structure. Since 1995, we have observed a rapid increase in cover by several large, dense patches of grass, mainly *Calamagrostis holmii* and *Arctagrostis latifolia,* in three of the four fertilized plots. These patches appear to be located on high spots in the soil surface (probably old, stabilized frost boils). We do not know the mechanism responsible for this latest change in species composition, nor do we know its implications for ecosystem processes. The important point, however, is that none of the changes that we observed over the first 15 yr of treatment are permanent or constant. Interactions among species composition, resource availability, and climate and microclimate cause continuous, long-term changes in both communities and ecosystems.

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