RESPONSES OF ARCTIC TUNDRA TO EXPERIMENTAL AND OBSERVED CHANGES IN CLIMATE[1]

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Abstract. We manipulated light, temperature, and nutrients in moist tussock tundra near Toolik Lake, Alaska to determine how global changes in these parameters might affect community and ecosystem processes. Some of these manipulations altered nutrient availability, growth-form composition, net primary production, and species richness in less than a decade, indicating that arctic vegetation at this site is sensitive to climatic change. In general, short-term (3-yr) responses were poor predictors of longer term (9-yr) changes in community composition. The longer term responses showed closer correspondence to patterns of vegetation distribution along environmental gradients. Nitrogen and phosphorus availability tended to increase in response to elevated temperature, reflecting increased mineralization, and in response to light attenuation, reflecting reduced nutrient uptake by vegetation. Nutrient addition increased biomass and production of deciduous shrubs but reduced growth of evergreen shrubs and nonvascular plants. Light attenuation reduced biomass of all growth forms. Elevated temperature enhanced shrub production but reduced production of nonvascular plants. These contrasting responses to temperature increase and to nutrient addition by different growth forms "canceled out" at the ecosystem level, buffering changes in ecosystem characteristics such as biomass, production, and nutrient uptake. The major effect of elevated temperature was to speed plant response to changes in soil resources and, in the long term (9 yr), to increase nutrient availability through changes in N mineralization. Species within a growth form were similar to one another in their responses to changes in resources (light or nutrients) but showed no consistent response to elevated temperature. Species richness was reduced 30–50% by temperature and nutrient treatments, due to loss of less abundant species. Declines in diversity occurred disproportionately in forbs, which are important for animal nutrition, and in mosses, which maintain soil thermal regime. There was no increased abundance of initially rare species in response to any treatment.

During our 9-yr study (the warmest decade on record in the region), biomass of one dominant tundra species unexpectedly changed in control plots in the direction predicted by our experiments and by Holocene pollen records. This suggests that regional climatic warming may already be altering the species composition of Alaskan arctic tundra.

Key words: arctic; climate change; diversity; light; nitrogen; phosphorus; productivity; temperature; tundra.

INTRODUCTION

Global warming is expected to be most pronounced at high latitudes (Hansen and Lebedeff 1987, Lashof and Ahuja 1990). In the Arctic, anticipated changes include warmer air and soil temperatures (Kane et al. 1992, Maxwell 1992), more rapid nutrient release from decomposing soil organic matter (Nadelhoffer et al. 1991), and increased summer cloudiness (Maxwell 1992), as sea ice melts and allows greater evaporation from the ocean. These environmental changes could profoundly affect tundra ecosystems. Productivity and growth-form composition of tundra consistently respond to nutrient addition, indicating widespread nutrient limitation (McKendrick et al. 1978, Shaver and

Chapin 1980, 1986, Shaver et al. 1986, Jonasson 1992). Similarly, changes in water table, which alter decomposition and nutrient availability, substantially alter the carbon balance of tundra microcosms (Billings et al. 1983). By contrast, net CO_2 flux from tussock tundra (i.e., the balance between production and decomposition) is remarkably insensitive to short-term (2–3 yr) changes in CO_2 concentration or temperature, presumably because of the strong nutrient limitation of plant production (Grulke et al. 1990, Oechel and Billings 1992). Likewise, in subarctic Sweden there is relatively little growth response to increased temperature (Havström et al. 1993, Parsons et al. 1994). These observations suggest an overriding influence of nutrient limitation on tundra production in the Low Arctic. Therefore, one might expect other environmental factors to affect production only if they alter nutrient availability (Jonasson 1992, Shaver et al. 1992).

In contrast to this apparent insensitivity of the tundra *ecosystem* to changes in variables other than nutrients, shoot growth by plants of *individual species* responds sensitively to changes in light, temperature, and nutrients, with each species showing different patterns of response (Chapin and Shaver 1985, Shaver et al. 1986, Parsons et al. 1994). The response of these species may cancel out at the ecosystem level due to a redistribution of resources among species in the community. Alternatively, the short duration (2 yr) of earlier studies may have shown initial environmental responses that cannot be sustained over the long term. To address these issues we initiated a long-term field experiment to examine the response of nutrient availability, biomass, and production of arctic tussock tundra to manipulations of light, temperature, and nutrients and to natural changes in environment that occurred during the study.

METHODS

Site and treatments

We conducted the study in 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 of arctic Alaska (68°38′ N, 149°34′ W, elevation 760 m). The site was deglaciated 60 000–100 000 yr BP, following the Itkillik I glaciation (Hamilton 1986, Walker et al. 1989). Vegetation on the site is dominated by approximately equal biomass of graminoids (mainly *Eriophorum vaginatum*), deciduous shrubs (mainly *Betula nana*), evergreens (mainly *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea*), and mosses (mainly *Sphagnum* spp., *Hylocomium splendens,* and *Aulacomnium* spp. (Shaver and Chapin 1991). Nomenclature follows Hultén (1968).

In June 1981 we established four replicate blocks in tussock tundra, each block containing four 5 × 20 m² plots separated by 1-m buffer strips. Within each block plots were randomly assigned to the following treatments: control, nutrient addition, elevated temperature, and light attenuation. Temperature was raised using a greenhouse placed over tundra. Light was reduced by shading. In the temperature plot of each block there were both a fertilized and a nonfertilized greenhouse, and in the light attenuation plot there was a single unfertilized shade frame. The area covered by each greenhouse and shade frame was 12 m², considerably less than the 100 m² of the control and fertilized plots. Because the major source of patchiness in tussock tundra is on the scale of decimetres, there was no difference in variance of biomass or production among our different-sized plots (data not shown). Greenhouses were built of transparent 0.15-mm (6 mil) plastic sheeting stretched over an A-shaped wooden frame that ranged in height from 10 cm at the side to 1 m in the center. Uneven microtopography allowed air circulation beneath the bases of the greenhouses, as in the open greenhouses of Havström et al. (1993). The plastic was replaced annually. Shade frames were identical to greenhouses but were covered with optically neutral shade cloth that removed 50% of incoming radiation (confirmed with a LiCor quantum sensor). Greenhouses and shade frames were placed on the plots each spring immediately after snow melt and removed each autumn from 1981 through 1989. The nutrient–temperature plots received 10 g/m² nitrogen (N) as NH_4NO_3, and 5 g/m² phosphorus (P) as P_2O_5 each spring immediately following snow melt. This is four times the annual N requirement for aboveground vascular production and 20 times the annual P requirement in this site (Shaver and Chapin 1991). The treatments were similar to those described by Chapin and Shaver (1985), except that in the earlier study the fertilizer was applied only once at 2.5 times the rate of the present study.

Environmental measurements

From 11 June to 13 July 1982, we measured, in one control, one elevated-temperature, and one light-attenuation plot, (1) photosynthetically active radiation (400–700 nm; control and temperature plots only) with LiCor quantum sensors, (2) air temperature 50 cm above the ground with a shaded thermocouple, (3) soil temperature at 10 cm depth in moss mats between *Eriophorum* tussocks, (4) soil temperature at 10 cm depth within tussocks (tussock temperature; control and temperature plots only), and (5) temperature in the litter on the top surface of tussocks (surface temperature). Measurements were made each minute, and hourly averages were recorded on a Campbell CR5 data logger. From these hourly values, we calculated the mean, minimum, and maximum values for each day and used these daily values to calculate the daily mean (± standard error) for the period of measurement. To determine patterns of environmental extremes, we calculated the mean irradiance and air temperature for each hour of the day on the five days with greatest and five days with least total irradiance. We measured thaw depths in early August 1989 at four randomly selected points per plot by pushing a probe from the moss surface to the bottom of thawed soil. We measured moisture gravimetrically in four soil samples per plot collected 10 cm beneath the moss mat in August 1989.

In early August 1991, at the time of maximum aboveground biomass, we measured CO_2 concentration 20 cm above the canopy in five warmed and five control plots in a site similar to and 1 km southwest of our study site, using a LiCor 6200 portable infrared gas analyzer three times during one clear day to span the daily range in irradiance. We measured relative humidity hourly in one heated and one control plot in 1991, recorded with a Campbell CR10 data logger. For comparison, we include data from 1980 on CO_2 concentration (measured with a gas chromatograph on four days encompassing a range of cloudiness in midseason)

and soil moisture (Chapin and Shaver 1985) from small greenhouses at the same site as the present study.

In the summer of 1988 and the preceding and following winters, we placed anion and cation exchange resins in bags made from nylon stockings 5 cm beneath the top of the organic horizon of each plot (Giblin et al. 1994). We extracted nutrients from these resins with 2 mol/L KCl and measured ammonium, nitrate, and phosphate colorimetrically by autoanalyzer. In early August 1989 we collected soils from the upper 5 cm of organic and upper 5 cm of mineral horizons of each plot and extracted one subsample with 2 mol/L KCl for analysis of ammonium and nitrate and a second subsample with 0.025 mol/L HCl for phosphate analysis. The organic horizon averages 20 cm depth.

Biomass harvests

We harvested plants from each of five randomly selected 20 × 20 quadrats per plot ($n = 20$ per treatment) at snow melt (21–22 May) in 1983 and at time of maximum aboveground biomass (late July/early August) in 1983 and 1989. The 1983 and 1989 harvests showed initial (3-yr) and long-term (9-yr) responses, respectively, of vegetation to our treatments and can be compared with the 1–2 yr responses of a single species (*Eriophorum*) in an earlier study (Shaver et al. 1986). We also sampled unmanipulated control plots in 1982 (Shaver and Chapin 1991), 1984, 1991, and 1992 (only *Eriophorum* and *Betula* in the last two years).

Detailed methods of quadrat sampling, the assignment of species to growth form, and precise definitions of tissue types are given by Shaver and Chapin (1991). Briefly, we separated live vascular-plant biomass by species and divided it into three categories of previous-years' biomass (old belowground stem, old aboveground stem, and old leaves) and four categories of current-year's biomass (new aboveground stem, new leaves, inflorescences, and new rhizome buds [graminoids only]). We consider all graminoid leaves as new biomass. We then separated graminoid leaves into blade and sheath and graminoid inflorescences into current year's and next year's inflorescence buds. At maximum aboveground biomass we included as live biomass all senescent leaves or leaf tips that had been alive earlier that season, as determined by leaf color. Because of the difficulty of harvesting fine roots from organic soils, we did not harvest roots in this study. All samples were weighed after oven-drying at 65°C. In 1989 nonvascular plants (mosses and lichens) comprised an additional category. Because forbs comprised only 0.4% of vascular-plant biomass, we include them with deciduous shrubs when data are presented by growth form.

We sampled nonvascular plants in early June 1984 before moss growth began, because these plants had been omitted from the 1983 harvest. We separated mosses by genus and lichens by group (foliose and fruticose) in 10 6.5-cm² randomly selected quadrats per plot. For two of the major moss genera (*Hylocomium splendens* and *Aulacomnium* spp.), where we could distinguish current from old growth (Tamm 1953), we separated moss into 1983 growth and previous years' biomass. New growth was 20 ± 2% of green biomass in both species in all except the nutrient treatment, where new growth was 30 ± 4% for *Hylocomium* and 37 ± 2% for *Aulacomnium,* and in the nutrient–temperature treatment, where there were too few mosses to measure. We estimated total moss production by assuming that all mosses had the same ratio of new growth to total live biomass as we measured in *Aulacomnium* and *Hylocomium.*

Using regressions of ln(mass per unit length) vs. age of individual stem segments (Shaver 1986), we estimated secondary (radial) stem growth rate in the shrubs *Salix pulchra* and *Ledum palustre,* in control and nutrient plots in 1985. We assumed that the annual percentage increase in stem mass was the same for *Betula* (the other common deciduous shrub) as for *Salix,* because *Betula* stems could not be aged. Evergreens other than *Ledum* in tussock tundra show insignificant secondary stem growth, as do belowground stems of all woody shrubs (Shaver 1986).

We made the following definitions: Aboveground plant parts include all sampled tissues (including graminoid leaf sheaths) except belowground stems and new rhizome buds. Current year's aboveground biomass includes current year's leaves, current year's stems, and inflorescences. At snow melt, these new-biomass categories consist of over-wintering buds (leaf sheaths and blades in the case of graminoids) produced the previous year. Apical aboveground growth is the increase in new aboveground biomass between snow melt and maximum aboveground biomass. Because we measured new biomass at snow melt only in 1983, we assumed the same proportional increase in new biomass between snow melt and maximum aboveground biomass when calculating apical aboveground growth in 1989.

We calculated aboveground net primary production (NPP) as the sum of apical aboveground growth (determined by quadrat harvests) and stem secondary growth (measured in a separate harvest). Most previous studies in tundra ignore stem secondary growth and amount of new biomass present at snow melt, so their NPP is comparable to our new biomass measured at maximum aboveground biomass. Although we measured stem secondary growth only in control and nutrient plots, we assumed that stem secondary growth in the nutrient–temperature plots was the same proportion of old-stem biomass as in the nutrient plot and the same proportion in the temperature and light plots as in controls. Because treatment effects on stem secondary growth rate were small (a nonsignificant 0–2% difference from control) compared to large variability in old-stem biomass among quadrats, most of the differences in secondary growth among treatments were

due to differences in biomass, so that any error in our assumptions about secondary stem growth should have minimal effect on estimates of NPP.

Nutrient analysis

For each tissue type, species, treatment, and sample date in 1983 and 1989, we lumped material from the five quadrats per plot. In 1983 we analyzed each plant part of each species separately. In 1989 we pooled samples by growth form (evergreen, deciduous, graminoid, lichen and moss), and in each of the three vascular-plant growth forms we pooled plant parts into new aboveground growth and old growth. We ground samples in a Wiley mill, digested them in selenous-sulfuric acid, and analyzed them colorimetrically by autoanalyzer for N (nitroferricyanide procedure) and P (phosphomolybdate procedure; Kedrowski 1983). We analyzed potassium, calcium, and magnesium in 1983 samples by atomic absorption, the latter two after addition of lanthanum chloride to reduce interference. We calculated nutrient pool sizes for each tissue type in each plot by multiplying each biomass value by its respective nutrient concentration. We calculated nutrient requirement as the pool of nutrients in apical aboveground growth, a measure that includes the nutrients supplied from both uptake and stored reserves.

Statistical analysis

Data did not deviate markedly from assumptions of normality, kurtosis, and equality of variance. We analyzed data as a two-way nested ANOVA, with nutrients and temperature as main effects, quadrats nested within blocks, and harvests as repeated measures. We compared the light treatment with the control using a separate one-way nested ANOVA with light as the main effect, quadrats nested within blocks, and harvests as repeated measures. We conducted these analyses with both log-transformed data (where treatment interactions are assumed to be multiplicative) and untransformed data (which assumes an additive model) and found similar patterns of significance. Therefore, we present significance levels for the untransformed data, which best describe the biology of the nutrient $\times$ temperature interaction.

We could not analyze NPP statistically because it was calculated from components measured in different samples (e.g., secondary stem growth, apical aboveground growth at snow melt, apical aboveground growth at maximum aboveground biomass, moss growth). Therefore, we interpret treatment effects on NPP cautiously, assuming that variability within and among treatments was similar to that observed in statistically analyzed parameters such as biomass and apical aboveground growth. We provide standard errors for parameters where possible.

RESULTS

Environment

Nutrient addition greatly increased the pools of extractable ammonium, nitrate, and phosphate, and the pools of these ions that accumulated on exchange resins during both winter and summer (Table 1). The surface nutrient addition was sufficient to exceed plant demands and allow leaching of exchangeable ammonium and phosphate into mineral soils. The lower concentration of nutrients on exchange resins during summer than in winter ($P < 0.05$) reflects a combination of seasonal differences in plant uptake, net mineralization, and duration of resin deployment. Nutrient addition reduced soil moisture slightly after 9 yr (Table 2), perhaps by stimulating net primary production (NPP) and its associated transpiration. The denser vascular-plant canopy or drier soils could explain the tendency of nutrient addition to reduce thaw depth in our study (Table 2) and to reduce soil temperature in nearby sites (J. Laundre, *unpublished data*).

The temperature treatment increased air, surface, and soil temperature, with less warming on cloudy days and no warming of nocturnal air temperature (Fig. 1, Table 2). Elevated temperature also increased soil thaw and reduced irradiance by 32%. Ventilation at the base of the greenhouse prevented detectable changes in relative humidity or CO_2 concentration. Elevated temperature caused an increase in exchangeable ammonium of the organic horizon and a consistent tendency to enhance the nutrients accumulated by exchange resins in soils (Table 1), suggesting a stimulation of mineralization.

The light attenuation treatment reduced irradiance by 50%, as intended, and tended to reduce thaw depth, but had no significant effect on temperature or soil moisture (Fig. 1, Table 2). Light attenuation increased exchangeable ammonium in organic soils and tended to increase nutrient pools on exchange resins in winter 1988–1989 (Table 1).

In summary, the treatments generally had the intended effect of increasing nutrients in the nutrient treatment, increasing temperature in the temperature treatment, and reducing light intensity in the light-attenuation treatment. In addition, temperature and light treatments tended to enhance nutrient availability, and the nutrient addition reduced soil moisture and thaw depth, indicating substantial indirect effects of our manipulations. The major complication was the reduced light intensity in the temperature treatment, which could offset any stimulatory effect of temperature.

Biomass

Nutrient addition had the largest effect of any treatment on total biomass (excluding roots) of most individual species (Table 3). After 3 yr, the biomass of graminoids (*Eriophorum* and *Carex*), mosses (especially *Aulacomnium*), and deciduous shrubs tended to increase, whereas after 9 yr, biomass of deciduous shrubs dominated the plots, and biomass of graminoids, evergreen shrubs, and nonvascular plants declined relative to the 3rd-yr harvest (Fig. 2, Tables 3 and 4). The deciduous shrub *Betula* dominated the long-term bio-

TABLE 1. Pool sizes of exchangeable nutrients on resin bags and in soil extracts of the treatment plots (mean $\pm$ 1 SE, $n = 8$).

| | Exchangeable nutrients‡ | | | | |
	Control	Nutrient	Temperature	Nutrient × temperature	Light
Resin bags (μmol/bag)					
Ammonium					
Summer 1988	3.9 ± 0.7	85 ± 33***	7.3 ± 3.4	139 ± 50	4.7 ± 1.0
Winter 1988–1989	7.6 ± 1.6	737 ± 298***	12.2 ± 6.5	1029 ± 191	17.6 ± 10.4
Nitrate					
Winter 1987–1988	5.3 ± 0.5	258 ± 59***	338 ± 223	202 ± 81†	4.9 ± 0.2
Summer 1988	4.8 ± 0.3	8.9 ± 1.9***	5.8 ± 0.9**	45 ± 11**	5.0 ± 0.2
Winter 1988–1989	3.6 ± 0.9	1292 ± 739	15.6 ± 12.6	510 ± 155	16.5 ± 13.3
Phosphate					
Winter 1987–1988	1.9 ± 1.0	239 ± 53***	7.3 ± 4.5	247 ± 68	0.2 ± 0.0
Summer 1988	0.3 ± 0.1	59 ± 18***	1.1 ± 0.9	41 ± 13	0.3 ± 0.1
Winter 1988–1989	1.9 ± 1.1	156 ± 56**	7.4 ± 5.8	187 ± 56	114 ± 46*
Soil extracts (μg/g soil)					
Ammonium-N					
Organic soil	2.2 ± 0.3	64 ± 24**	3.3 ± 0.7*	412 ± 124*	6.9 ± 1.8*
Mineral soil	1.4 ± 0.4	5.6 ± 1.0***	1.4 ± 0.3	6.3 ± 0.9	1.8 ± 0.6
Nitrate					
Organic soil	0.0 ± 0.0	3.4 ± 1.6**	0.0 ± 0.0	167 ± 65**	0.1 ± 0.0
Mineral soil	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	1.0 ± 0.5	0.1 ± 0.1
Phosphate					
Organic soil	0.7 ± 0.2	252 ± 169**	1.7 ± 0.9	282 ± 98	3.8 ± 1.9
Mineral soil	0.1 ± 0.0	1.3 ± 0.6**	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0

Level of significance of treatment effects: † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Other differences are not statistically significant. Nutrient and temperature effects were tested with a 2 × 2 ANOVA and light effects with a one-way ANOVA.

mass response to nutrients, with mosses and lichens being nearly eliminated after 9 yr. Except for graminoids, all species of a given growth form were similar to one another in their nutrient responses. For example,

both deciduous shrub species were stimulated by nutrients, whereas both evergreen shrub species were inhibited (Table 3). Because the large stimulation of *Betula* was counterbalanced by declines in other growth

TABLE 2. Environmental characteristics of the treatment plots (mean $\pm$ SE).

Parameter	Control	Nutrient	Temperature	Nutrient × Temperature	Light
Air temperature (°C)					
Daily mean	11.2 ± 1.0	···	14.7 ± 1.0**	···	12.1 ± 1.0
Daily maximum	17.4 ± 1.2	···	27.4 ± 1.6***	···	18.3 ± 1.2
Daily minimum	4.4 ± 0.7	···	3.8 ± 0.6	···	5.2 ± 0.7
Surface temperature (°C)	12.0 ± 0.8	···	17.0 ± 0.9***	···	12.4 ± 0.8
Soil temperature (°C)	3.6 ± 0.2	···	5.8 ± 0.5***	···	3.8 ± 0.3
Tussock temperature (°C)	6.3 ± 0.5	···	9.1 ± 0.7**	···	···
Thaw depth (cm)	38.3 ± 3.0	31.7 ± 2.7	42.6 ± 2.2***	43.5 ± 1.7†	31.6 ± 2.5†
Soil moisture (% dry mass)					
1980	946 ± 98	978 ± 181	1015 ± 135	···	845 ± 65
1989	479 ± 23	432 ± 27*	610 ± 60	424 ± 86	465 ± 26
Irradiance (mol·m^{-2}·d^{-1})	46.0 ± 2.2	···	31.5 ± 1.4***	···	23.0‡
Relative humidity (%)	68.1 ± 1.5	···	67.0 ± 2.4	···	···
CO$_2$ concentration, μL/L					
1980	332 ± 9	···	334 ± 11	···	···
1991	343 ± 1	···	341 ± 2	···	···

Level of significance of treatment effects: † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Other differences are not statistically significant. Nutrient and temperature effects on thaw depth and soil moisture were tested with a 2 × 2 ANOVA. All other comparisons were one-way ANOVAs.

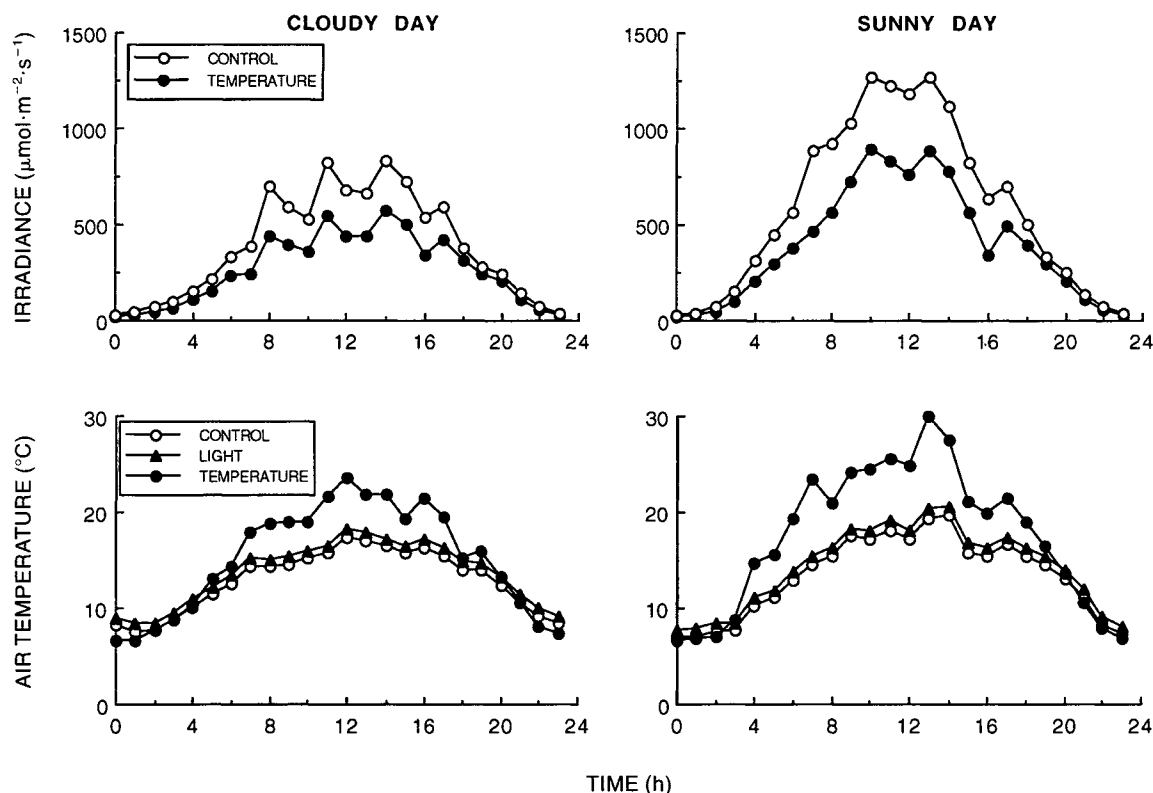‡ Spot measurements indicate 50% reduction from control.

FIG. 1. Daily pattern of irradiance (photosynthetically active radiation, 400–700 nm) and air temperature averaged for 5 clear and 5 cloudy days.

forms, particularly nonvascular plants, there was no significant nutrient effect on total biomass at the ecosystem level (Table 4, Fig. 2).

The small decline in total biomass with increased temperature was also the result of compensatory changes by individual species (Fig. 2, Tables 3 and 4). The increased biomass of *Eriophorum* and *Ledum* compensated for the decreased biomass of *Carex* and mosses after 9 yr. The contrasting responses of the two graminoids, *Eriophorum* and *Carex*, were typical of the general pattern in which species of a given growth form often differed in their responses to temperature.

In the nutrient–temperature treatment the threefold increase in *Betula* biomass after 9 yr coincided with biomass declines of all other species except *Rubus* (the other deciduous shrub; Tables 3 and 4, Fig. 2). The abundant *Betula* litter in this treatment covered the mosses and lichens almost completely, contributing to their elimination from these plots. In general, the combined effect of increased temperature and nutrients was to speed up plant response to nutrients. For example, *Carex, Rubus, Ledum* and the mosses were stimulated less (or even inhibited) in the nutrient–temperature treatment compared to the nutrient treatment after 3 yr, and these species declined even more strongly in the nutrient–temperature treatment after 9 yr than in the nutrient-only treatment.

A 50% reduction in irradiance in the light attenuation treatment had the same effect on each vascular plant species as did the stimulation of a *Betula* canopy in the temperature–nutrient treatment, i.e., all species tended to decline in biomass except for the shade-tolerant understory *Rubus*, which tended to increase in both the nutrient–temperature and light-attenuation treatments (Tables 3 and 4, Fig. 2). The less pronounced decline in nonvascular plants in the light attenuation (−34%) than in the nutrient–temperature treatment (−100%) could reflect either the intense shading by *Betula* or the additional impact of its leaf litter on moss growth in the nutrient–temperature treatment.

In summary, resources required for growth (i.e., nutrients and light) appeared to be more critical than temperature in determining plant biomass in tussock tundra. Although there were relatively modest effects of treatments on total ecosystem biomass (coefficient of variation across treatments = 20%), this was the net result of a major redistribution of resources among component species and growth forms in the ecosystem. (Coefficient of variation for biomass of the six major vascular-plant species across treatments averaged 67 ± 5%.) Growth form was a good predictor of response to nutrients but not to temperature.

During our 11-yr study (1982–1992), the warmest decade on record (Trenberth 1990, Oechel et al. 1993),

TABLE 3. Total peak-season biomass (excluding roots) of major tussock-tundra species in 1983 and 1989 (mean ± 1 SE, $n = 4$ replicate blocks, 5 quadrats per plot).

Growth form/species/year	Total biomass (g/m²)				
	Control	Nutrient	Temperature	Nutrient × temperature	Light
Graminoid					
Eriophorum vaginatum					
1983	145 ± 34	188 ± 48	177 ± 64	97 ± 19†	67 ± 21†
1989	51 ± 12	66 ± 24†	101 ± 34	5 ± 4*	39 ± 13
Carex bigelowii					
1983	43 ± 11	77 ± 17†	40 ± 18	62 ± 15	43 ± 11
1989	54 ± 15	28 ± 16	22 ± 8†	12 ± 5	33 ± 9
Deciduous					
Betula nana					
1983	159 ± 32	250 ± 37**	125 ± 8	306 ± 39	119 ± 32
1989	267 ± 67	694 ± 93***	274 ± 55	744 ± 92	109 ± 19†
Rubus chamaemorus					
1983	24 ± 10	49 ± 14	25 ± 5	38 ± 10	22 ± 8
1989	14 ± 4	78 ± 20	33 ± 12	15 ± 4	26 ± 8
Evergreen					
Ledum palustre					
1983	176 ± 22	170 ± 30	133 ± 43	155 ± 27	217 ± 40
1989	185 ± 31	118 ± 33***	271 ± 31	47 ± 14***	147 ± 13
Vaccinium vitis-idaea					
1983	136 ± 17	102 ± 13†	159 ± 16	112 ± 27	136 ± 13
1989	129 ± 15	41 ± 13***	160 ± 23*	3 ± 2*	60 ± 7**
Mosses‡					
1983					
Sphagnum spp.	133 ± 33	187 ± 50	163 ± 16	100 ± 44	81 ± 21
Aulacomnium spp.	42 ± 15	86 ± 21	57 ± 19	30 ± 7*	50 ± 7
Hylocomium splendens	38 ± 11	39 ± 16	24 ± 14†	15 ± 5	33 ± 10

Level of significance of treatment effects: † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Other differences are not statistically significant. Nutrient and temperature effects were tested with a 2 × 2 ANOVA and light effects with a one-way ANOVA.
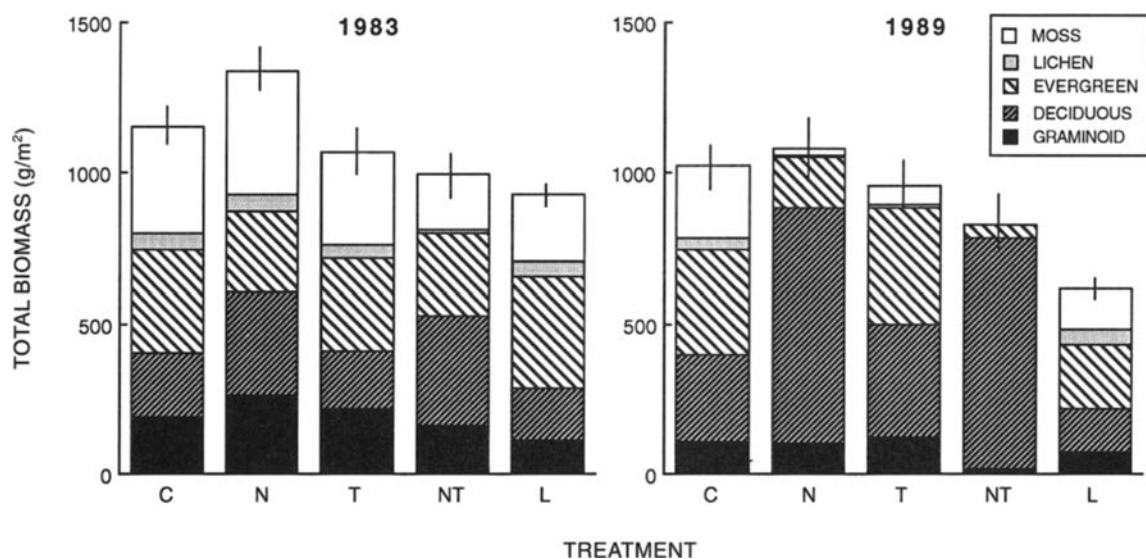
‡ Not separated by species in 1989.

FIG. 2. Total peak-season biomass (excluding roots) of tussock-tundra vegetation by growth form in response to environmental manipulations measured 3 and 9 yr after initiation of treatments. Data are means and SE, $n = 4$ blocks, 5 quadrats per plot. Treatments are control (C), nutrient (N), temperature (T), nutrient–temperature (NT), and light attenuation (L).

TABLE 4. Statistical significance of treatment effects on total biomass, aboveground biomass, and aboveground apical growth. Abbreviations for treatments are described in Fig. 2, with successive harvests at different times (t) used as repeated measures in the ANOVA. Levels of significance as shown in Table 1, $n = 4$ replicate blocks, 5 quadrats per plot. Lack of statistical significance ($P > 0.1$) is also indicated ($\cdots$).

Parameter/ growth form	Level of significance								
	N	T	N × T	L	t	N × t	T × t	N × T × t	L × t
Total biomass									
Total	...	**	*	***	*	...	...	...	†
Nonvascular	***	***	...	**	***	*	...	***	...
Vascular	*	...	†	***	...	...	...	...	*
Deciduous	***	...	...	**	†	**	...	...	...
Graminoid	...	†	**	*	*	...	...	...	...
Evergreen	***	...	...	...	*	***	...	**	**
Aboveground biomass									
Total	*	**	...	***	*	...	...	*	...
Nonvascular	***	***	...	**	***	*	...	***	...
Vascular	***	...	...	**	...	†	...	...	...
Deciduous	***	...	...	...	**	***	...	...	...
Graminoid	...	...	**	*	*	...	...	...	...
Evergreen	***	...	...	†	*	***	...	**	**
Apical aboveground growth									
Total	***	...	**	***	**	†	...	...	...
Nonvascular	...	***	...	**	***	***	*	***	...
Vascular	***	...	*	**	...	...	...	...	...
Deciduous	***	*	†	...	***	***	...	...	...
Graminoid	...	...	**	*	†	...	...	...	...
Evergreen	***	†	...	†	...	***	...	...	**

total biomass of the dominant sedge, *Eriophorum,* was reduced to 30% of its initial value in unmanipulated control plots, and *Betula* biomass tended to be highest in 1989 (the warmest year on record), as predicted by our manipulations simulating a warmer, more fertile environment (Fig. 3). No other vascular-plant species showed significant change in biomass on control plots during the study, although mosses, *Carex,* and *Vaccinium* (but not *Ledum*) tended to change biomass in control plots from 1983 to 1989 in the same directions as predicted by the 1983 nutrient–temperature treatment. These results suggest that regional climatic warming is already changing the abundance of dominant species in tussock at Toolik Lake.

Aboveground production

We analyzed the production responses to our manipulations in terms of apical aboveground growth, which we analyzed statistically, and aboveground net primary production (NPP), which includes all components of growth (apical growth of vascular plants and mosses plus stem secondary growth), but could not be analyzed statistically. In general, apical growth and NPP showed similar responses to our manipulations, but NPP was more sensitive than apical growth to treatments that altered deciduous shrubs, the growth form with the greatest secondary stem growth.

Aboveground NPP (Fig. 4) and apical growth (Fig. 5, Table 4) showed greater response than did biomass (Fig. 2) to treatments, particularly to nutrients. As with biomass, NPP and apical growth of graminoids, nonvascular plants, and deciduous shrubs increased after

3 yr of nutrient addition, whereas after 9 yr *Betula* dominated, and graminoids, evergreen shrubs, and nonvascular plants declined relative to the 3rd-yr harvest. Total ecosystem NPP and apical growth of graminoids increased in the temperature treatment and declined in the nutrient–temperature treatment (relative to the fertilized plots), causing a strong nutrient–temperature interaction in both 1983 and 1989. Evergreen- and deciduous-shrub growth increased in response to temperature, and nonvascular growth declined in response to temperature, particularly after 9 yr. Light attenuation reduced growth of all growth forms except deciduous shrubs. As with biomass, all species of a growth form responded similarly to a change in resources (nutrients or light), but there was no consistent temperature response among species within a growth form.

Because each species showed a different pattern of response to our manipulations, there was less variation in ecosystem NPP among treatments (coefficient of variation = 33%) than in NPP of the six major vascular-plant species (average coefficient of variation of 87 ± 12%). NPP of a given species varied substantially more across treatments after 9 yr than after 3 yr, indicating that treatment effects became more pronounced with time.

Species richness

In control plots, there were two deciduous, two evergreen, and two graminoid species among the six most abundant vascular-plant species (Fig. 6), confirming the high growth-form diversity of tussock tundra (Shaver and Chapin 1991). Most rare species were deciduous
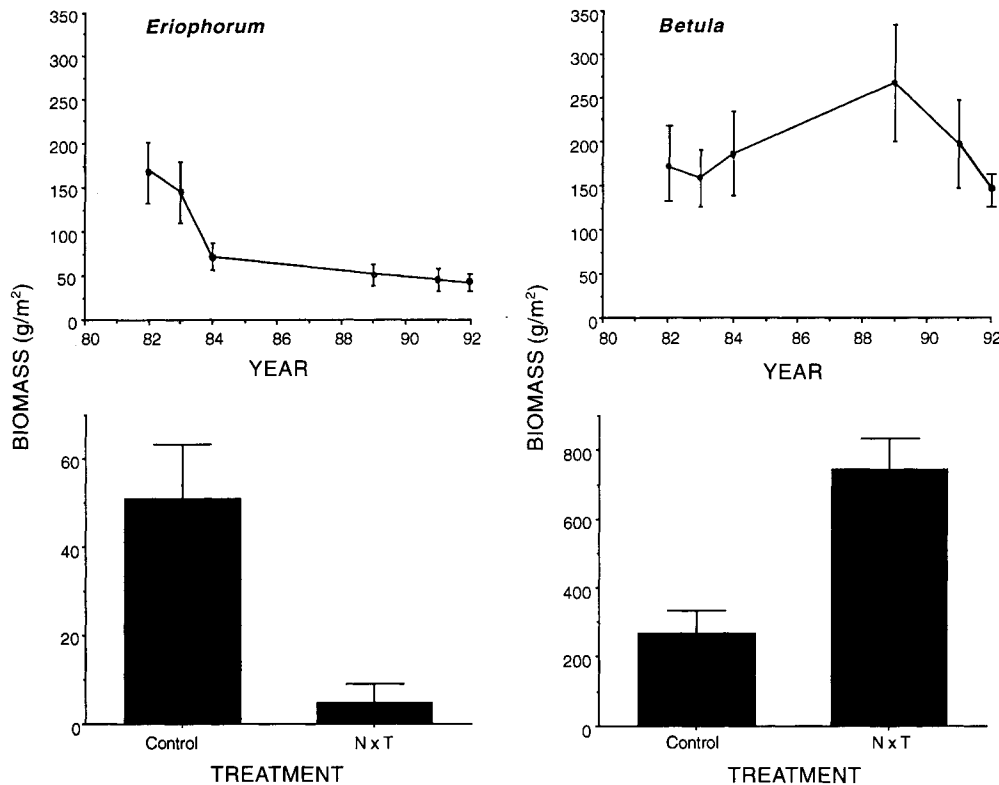
FIG. 3. Time course of maximum total biomass of *Eriophorum* and *Betula* in unmanipulated control plots from 1982–1992. Data are means and SE, *n* = 4 blocks, 5 quadrats per plot. Also shown is the biomass response of these two species after 9 yr of simulated climatic warming with increased mineralization.

forbs. After 3 yr, the only effect of manipulations on species richness was the loss or greatly reduced biomass of a few rare species of forb or grass in the nutrient and nutrient–temperature treatments. However, after 9 yr the strong dominance by *Betula* was associated with loss of 30–50% of the species in these treatments. Evergreen shrubs and understory forbs declined more strongly than other species or disappeared
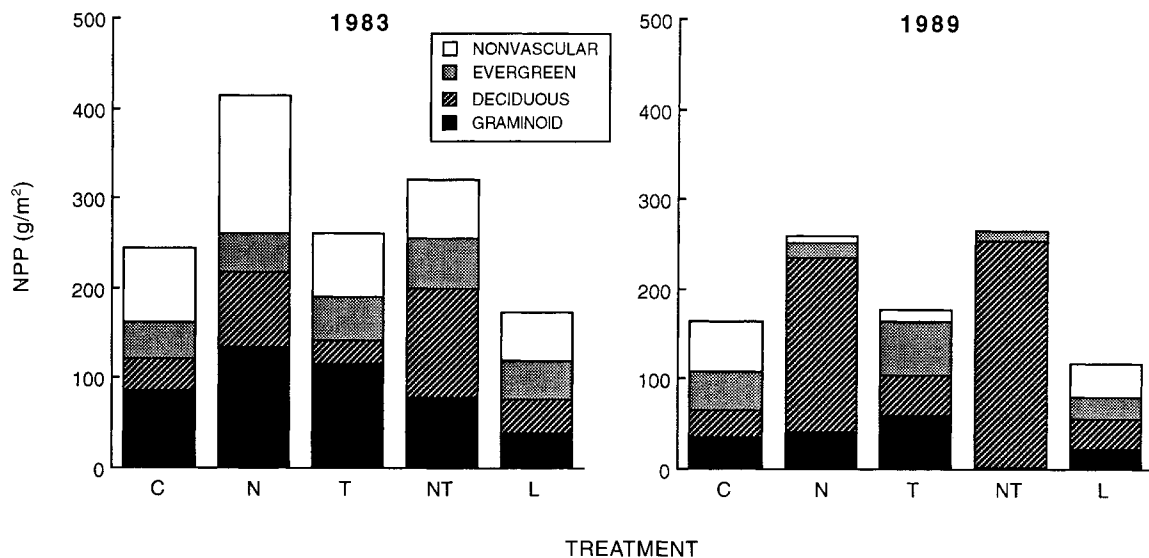

FIG. 4. Total aboveground NPP of tussock-tundra vegetation in response to environmental manipulations, measured 3 and 9 yr after initiation of treatments. Treatment symbols as in Fig. 2.
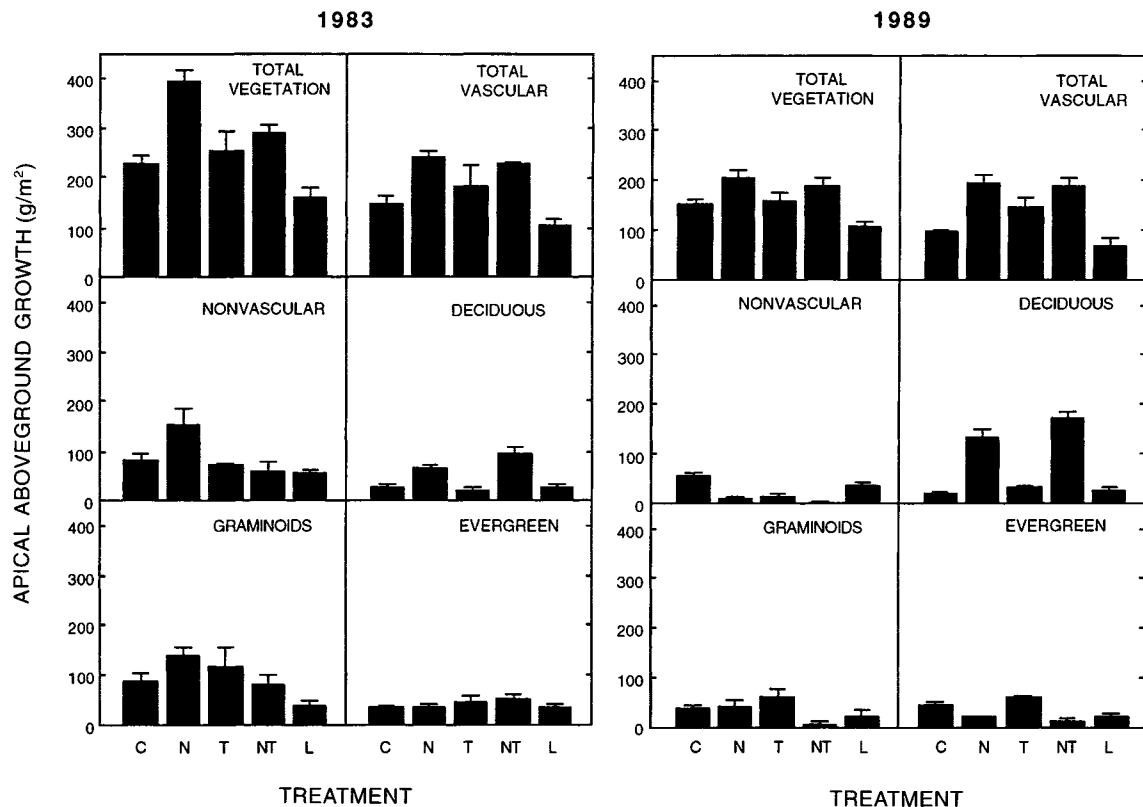
FIG. 5. Apical aboveground growth of tussock-tundra vegetation in response to environmental manipulations, measured 3 and 9 yr after initiation of treatments. Treatment symbols as in Fig. 2. Statistics in Table 4.

entirely. Elevated temperature increased the dominance of the four species that were initially most abundant and decreased abundance of or eliminated the third of the community that was initially least abundant, particularly forbs. After 9 yr, light attenuation decreased the biomass of all species, most strongly for dominant species and least for rare species. Thus, the large decrease in species richness and increase in dominance in the temperature and nutrient–temperature treatments must reflect direct and indirect effects of temperature rather than of the 30% reduction in irradiance in these treatments (Table 2). In summary, the six species of three growth forms that were most common in control plots remained most common in all treatments. The loss of species richness resulted from loss of rare species, and none of the species that were initially rare gained long-term dominance. The treatments simulating climate warming (temperature and nutrient–temperature treatments) showed greatest species loss after 9 yr.

Nutrients

In response to increased nutrients, the N pool in the vegetation doubled after 3 and 9 yr, and the P pool tripled (Fig. 7). This increment corresponds to 62% of the N and 18% of the P added during the first 3 yr. All growth forms increased their N and P pools in response

to nutrient addition during the first 3 yr. Nutrient accumulation was most pronounced in mosses because of their direct contact with the applied fertilizer and least pronounced in evergreen shrubs, which have slow rates of nutrient uptake (Chapin and Tryon 1982). Even though evergreens declined in biomass continuously for 9 yr with nutrient addition (Fig. 2), during the first 3 yr they increased their N and P accumulation (Fig. 7). Similar results were found with individual species, which all initially increased their N and P pools in response to nutrient addition. This response was most pronounced in *Aulacomnium,* a moss characteristic of eutrophic habitats, and least pronounced in the evergreens *Ledum* and *Vaccinium* (data not shown).

Although K, Ca, and Mg were not included in the fertilizer, pools of these elements in the vegetation increased 29, 73, and 36%, respectively, in response to fertilizer addition after 3 yr (Fig. 8), greatly exceeding the 16% increase in total biomass (Fig. 2). This demonstrates that demand for nutrients, caused by increased NPP, strongly influenced absorption of ions other than N and P. Graminoids and deciduous shrubs accounted for the increases in K and Mg, but mosses also contributed strongly to the increased Ca pool.

Surprisingly, plant nutrient pools in the nutrient–temperature treatment were lower than those in the
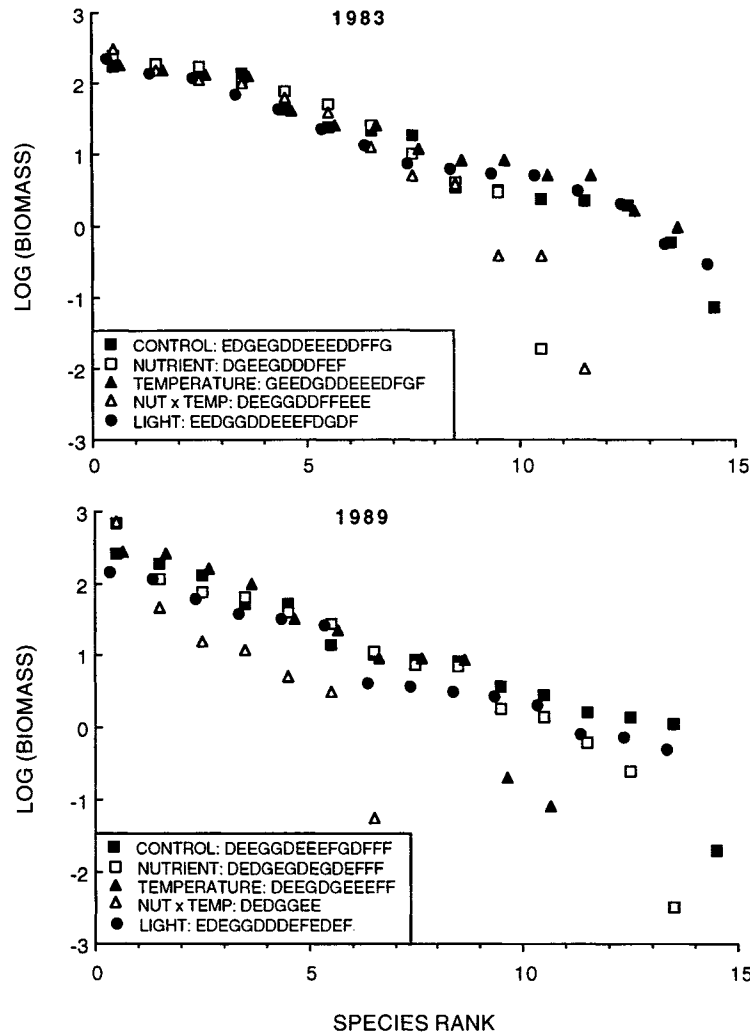
FIG. 6. Vascular-plant biomass dominance-diversity curves sampled 3 and 9 yr after initiation of treatments. Also shown is the sequence in abundance of growth forms represented by each species in each treatment: evergreen (E), deciduous (D), graminoid (G), and forb (F).

nutrient treatment (32 and 38% less for N and P, respectively; Fig. 7), to a greater degree than biomass reduction (25%; Fig. 2). This reflected a decrease relative to the nutrient treatment in both biomass (Table 3) and N and P concentration (data not shown) of *Eriophorum* and mosses, the species that were negatively affected by the nutrient–temperature treatment. Thus, the higher N and P availability in soils of the nutrient–temperature treatment compared to nutrient treatment (Table 1) resulted from less nutrient uptake by vegetation.

Elevated temperature alone caused no change in nutrient pools in vegetation after 3 or 9 yr (Fig. 7), indicating that there was no net transfer of nutrients from soil to plants in the greenhouse. However, after 9 yr nonvascular plant N and P pools were less than half the pools in control plots, with the remaining nutrients being transferred to vascular plants. Thus,

elevated temperature caused a substantial redistribution of nutrients from nonvascular to vascular plants. Although light attenuation reduced biomass, it had little effect on nutrient accumulation except a tendency for cations to decline in graminoids after 3 yr (Fig. 8).

Nutrient requirement for NPP (uptake plus redistribution from reserves) was altered more strongly than standing stocks of nutrients, particularly in graminoids and deciduous shrubs (Figs. 7 and 9), indicating that our treatments had much greater impact on nutrient availability and turnover than changes in the standing stocks would suggest. For example, in graminoids and deciduous shrubs, nutrient addition tripled annual N requirement and caused a 7–8-fold increase in P requirement. Even in the temperature treatment, where there was no treatment effect on nutrient pools in vegetation after 3 yr, there was a trend
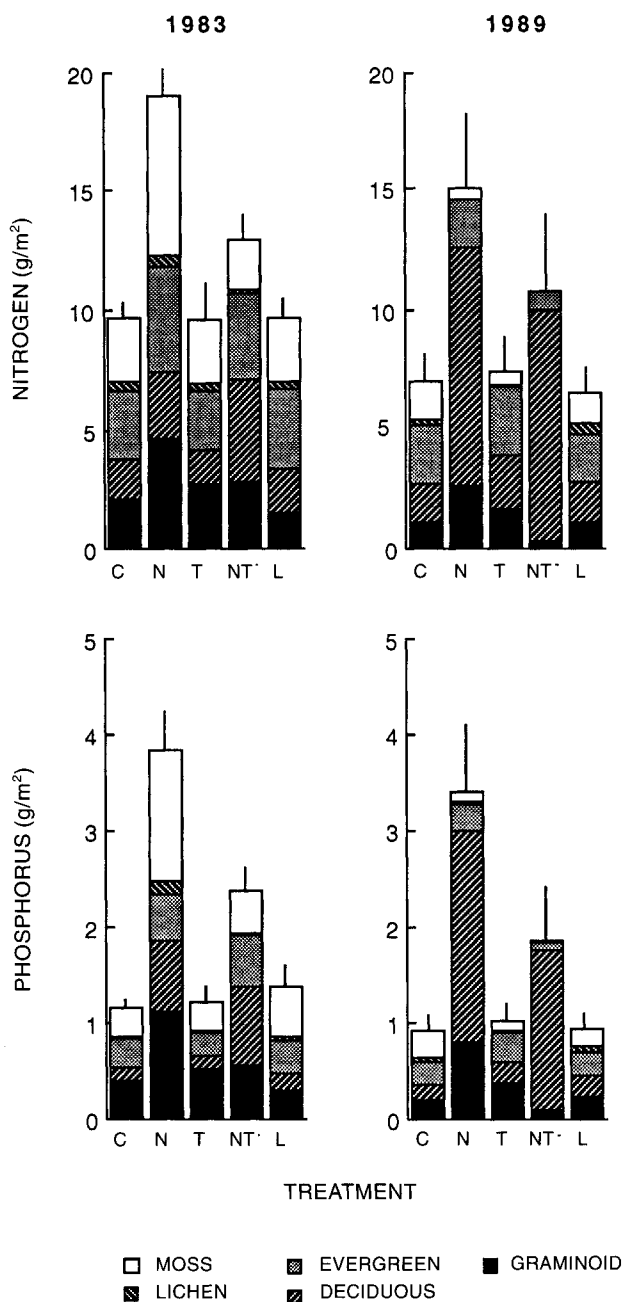
FIG. 7. Total nitrogen and phosphorus pools in peak-season biomass of tussock-tundra vegetation in response to environmental manipulations, measured 3 and 9 yr after initiation of treatments. Treatment symbols as in Fig. 2.

(13–21%) toward increased N and P requirement relative to the control, suggesting enhanced mineralization. This was the most pronounced in the vascular plants. Light attenuation tended to reduce N uptake by vascular plants after 9 yr, perhaps explaining the increased exchangeable ammonium in the shade treatment. We found similar treatment effects on nutrient uptake, when we calculated uptake as the increase in

total-plant nutrient pool between snow melt and time of maximum aboveground biomass in 1983 (data not shown), suggesting that the treatment effects on nutrient requirement (Fig. 9) reflect differences in uptake rather than the extent to which species draw nutrients from stored reserves to support growth.

DISCUSSION

Environment

Although our manipulations altered primarily those variables that we intended to change, potential complications are similar to those expected to accompany natural climatic warming. By using technologically simple manipulations, we could, for the first time, observe long-term vegetation responses. The 3.5°C temperature increase in our greenhouses is within the 3°–8°C range of increased air temperature expected in the Arctic within the next 50 yr (Hansen and Lebedeff 1987, Maxwell 1992). The effects of our temperature treatment and natural climatic warming are complicated by increases in soil temperature, thaw depth, and nutrient availability, and a decline in irradiance (Maxwell 1993), and should not, therefore, be considered the result of simple changes in air temperature. The reduced thaw depth in the shade treatment and the reduced soil moisture accompanying greater biomass in the fertilized plots are expected indirect effects of these treatments that would accompany similar changes caused by altered climate. The increased nutrient availability in the shade treatment reflected reduced nutrient uptake by vegetation, as plant growth became limited by light rather than nutrients.

The increased nitrogen availability and increased nutrient accumulation by vascular plants with elevated temperature suggests that increased nutrient availability was an important indirect effect of warming. The trend toward increased nutrient availability during winter when greenhouses were removed was surprising and suggests that one mechanism by which the temperature treatment affected decomposition was through changes in species composition and litter quality rather than direct thermal effects on decomposition. Alternatively, more active plant uptake in the temperature treatment in summer could have competed with exchange resins and maintained available nutrients at low levels. Indirect effects of temperature on litter quality and decomposition occur gradually and could explain why greenhouses similar to ours have little or no effect on mineralization or nutrient availability in their first 2–3 yr at Toolik Lake (S. E. Hobbie, *unpublished data*) or in Sweden (Jonasson et al. 1993), although the lack of a greenhouse effect on nutrient availability in these studies could be explained by small effects of these greenhouses on soil temperature. The long time lag (>3 yr) between initiation of treatment and ecosystem response indicates the need for long-term field experiments in predicting the effects of climatic change.
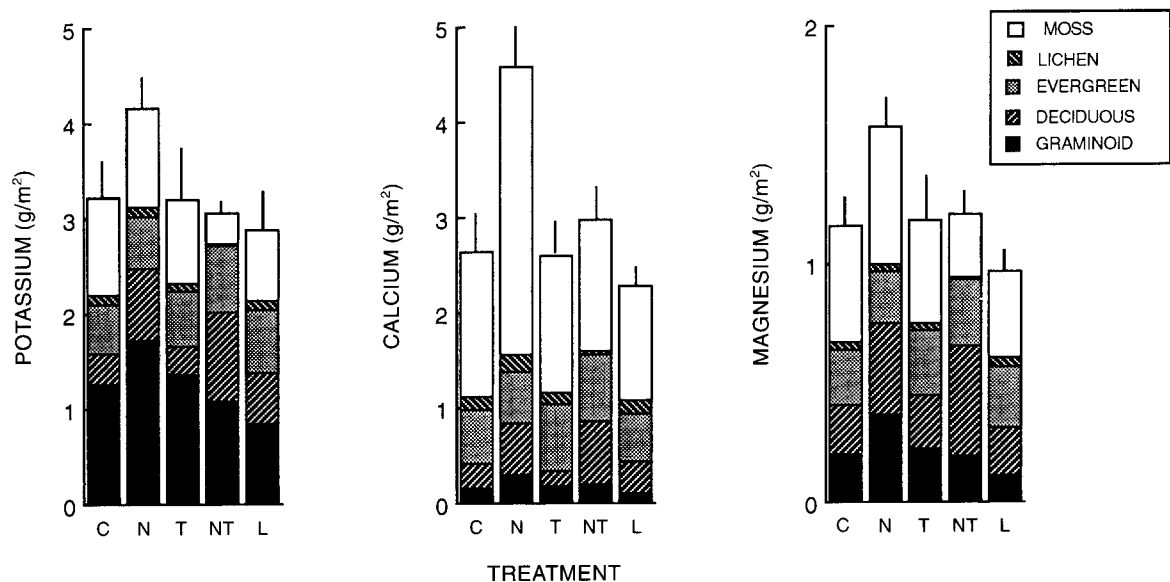
FIG. 8. Total potassium, calcium, and magnesium pools in peak-season biomass of tussock-tundra vegetation in response to environmental manipulations, measured 3 yr after initiation of treatments. Treatment symbols as in Fig. 2.

Our temperature treatment produced no detectable artifacts such as soil drying, diurnal depletion of atmospheric CO_2, a decline in relative humidity that might induce stomatal closure, or direct heat damage to plants on warm sunny days. In no case did we detect wilting, declines in photosynthetic potential (F. S. Chapin, III, et al., *unpublished data*), or other symptoms of heat stress in the greenhouses. Similar greenhouses reduced relative humidity in drier high-arctic and subarctic sites (Havström et al. 1993, Wookey et al. 1993). Although the greenhouses excluded rain, their small size allowed soil moisture to be maintained at control levels by lateral water movement over permafrost, a source that can be substantial in tussock tundra (Chapin et al. 1988). The lack of an effect of the temperature treatment on CO_2 concentration or relative humidity presumably reflects substantial air circulation at the base of the greenhouses. Similar greenhouses have not affected CO_2 concentration more than a few microlitres per litre under a wide variety of light and temperature conditions in environments ranging from alpine to High Arctic (Havström et al. 1993, S. E. Hobbie, *unpublished data*). These greenhouses exhibit small increases (10%) in relative humidity during the day and small decreases (10%) at night, with no change in average relative humidity (J. Laundre and G. R. Shaver, *unpublished LTER data*), indicating that greenhouses would not cause drought-induced stomatal closure during the day.

Biomass and production

Our experimental manipulations altered biomass, production, species richness, and species composition of tussock tundra in less than a decade. The 3-yr stim-

ulation of biomass and production in deciduous shrubs and graminoids by nutrient addition is commonly observed in vascular plants of tundra in response to fertilizer (McKendrick et al. 1978, Shaver and Chapin 1980, Jonasson 1992), animal carcasses and feces (Batzli et al. 1980, McKendrick et al. 1980), fire (Wein and Bliss 1973), or human disturbance (Chapin and Shaver 1981), indicating widespread nutrient limitation of plant growth. However, the eventual dominance of fertilized plots by deciduous shrubs and the decline in evergreen shrubs that we report here is more consistent with descriptive ordinations of undisturbed tundra vegetation, where high-fertility sites are dominated by deciduous species and low-fertility sites by evergreens (Webber 1978, Shaver and Chapin 1991), as found in many woody-plant-dominated biomes (Beadle 1966, Chapin 1980). Similarly, in subarctic Sweden, nutrient addition consistently enhanced leaf area of deciduous shrubs and graminoids but not of most evergreen shrubs (*Empetrum* and *Loiseleuria,* but see *Dryas*) and lichens (Jonasson 1992). From these results, we predict that increased nutrient availability caused indirectly by climatic warming should increase the abundance of deciduous shrubs relative to evergreen shrubs and nonvascular plants. The more rapid decomposition and nutrient cycling that occur in deciduous than in evergreen communities (Flanagan and Van Cleve 1983, Berendse and Jonasson 1992) would then create a positive feedback to magnify initial changes in nutrient supply and species composition (Chapin 1991, Hobbie 1992).

Inclusion of nonvascular plants in our study produced results that conflict with conclusions that we and other ecologists have made about the predominant im-
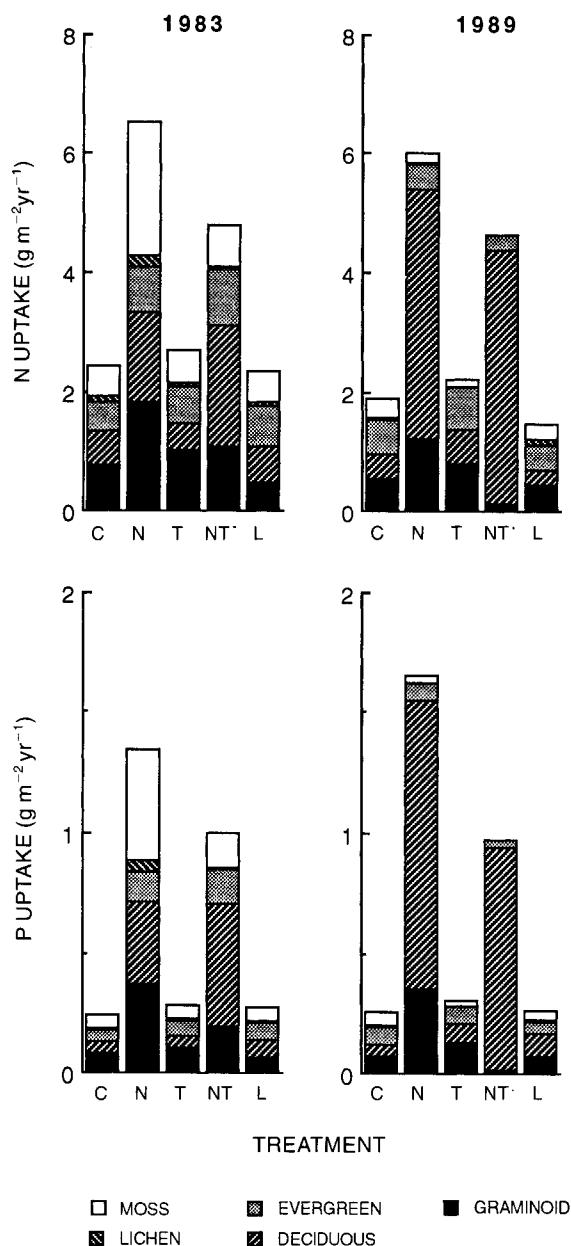
FIG. 9. Nitrogen and phosphorus uptake into apical aboveground growth of tussock-tundra vegetation in response to environmental manipulations, measured 3 and 9 yr after initiation of treatments. Treatment symbols as in Fig. 2.

sponse to nutrient addition in our study despite a stimulation of production reflects the replacement of mosses, lichens, and evergreen shrubs, which have slow turnover of leaves and stems, by deciduous species with higher production : biomass ratios (Shaver and Chapin 1991) and more rapid tissue turnover by each species under conditions of high fertility (Chapin 1980). Graminoids initially responded rapidly to nutrient addition but were shaded out by taller deciduous shrubs after 9 yr. To the best or our knowledge, this is the first study to document the long-term biomass response of a complete tundra plant community, including nonvascular plants, to nutrient addition. In subarctic Sweden, vascular plants were a larger proportion of plant cover than in our site, and a strong vascular-plant response to nutrient addition after 4 yr, therefore, translated into a strong community response (Jonasson 1992).

The relatively small responses of ecosystem biomass and NPP to our nutrient and temperature manipulations resulted from large opposing responses by individual species, as seen previously (Lauenroth et al. 1978, Chapin and Shaver 1985). This stability of ecosystem NPP follows logically from physiological differences among species and resulting shifts in competitive balance with a change in environment (Tilman 1988). This is seen in large fluctuations in NPP of individual species but small fluctuations in ecosystem NPP in response to our manipulations (Chapin and Shaver 1985), geographic variation in environment (Webber 1978), annual variation in weather (Lauenroth et al. 1978, Chapin and Shaver 1985) or longer term changes in climate (Davis 1981, COHMAP 1988). Because of this compensation at the ecosystem level, we expect ecosystem properties such as NPP or rates of biogeochemical cycling in closed communities to be less sensitive to climatic change than would be predicted from extrapolations of environmental responses of single species (Pastor and Post 1988, Prentice and Fung 1990).

The lack of a strong response to the temperature treatment at the ecosystem level could reflect limitation of NPP by nutrient supply rather than temperature, a stimulation of plant respiration by temperature, or a confounding of some unmeasured temperature stimulation by the 32% reduction in light intensity. When the MBL-GEM ecosystem model (Rastetter et al. 1991) was used to separate the light and temperature effects in our greenhouse treatment, the 3.5°C temperature increase was estimated to increase biomass by 20% counterbalanced by a simultaneous 11% biomass decline due to light attenuation (R. B. McKane et al., *unpublished manuscript*). Because increased cloudiness is expected to accompany climatic warming (Maxwell 1992), the light reduction in the greenhouse could be a reasonable simulation of warmer conditions in the Arctic.

After 9 yr, the strong negative effect of light attenuation on NPP and biomass of all species (except the shade-tolerant *Rubus*) and the increase in nutrient avail-

portance of nutrient limitation in tundra. Although productivity of vascular plants is nutrient-limited, this is compensated by reduction in biomass of nonvascular plants, which in Alaskan spruce forests are not nutrient-limited (Skre and Oechel 1979). In subarctic Sweden, lichens always declined with nutrient addition, and mosses declined with nutrient addition in graminoid- and deciduous-shrub tundra but increased in heath and open frost-polygon tundra (Jonasson 1992). The lack of a long-term (9-yr) increase in total biomass in re-

ability indicated a switch from nutrient to light limitation of plant growth. Similarly, light limits growth of alpine plants more strongly than does temperature (Körner 1982). *Sphagnum* responded positively (in terms of height growth) to light attenuation after 1 yr (Murray et al. 1993) but responded negatively in biomass after 3 yr (our results). This difference in response could reflect an etiolation response that is evident in height but not biomass, or it could indicate that an initial growth response was a poor predictor of the 3-yr growth response.

Unmeasured changes in roots (20% of biomass and 35% of production in tussock tundra; Shaver and Chapin 1991) should not modify greatly our conclusions. If allocation between root and shoot production changed according to patterns observed in other studies, we would have underestimated the vascular-plant decrease in production in response to light attenuation, due to decreased root allocation (Brouwer 1962, Davidson 1969), underestimated the increase in production in response to temperature due to increased root allocation (Kummerow and Ellis 1984), and overestimated the increase in production in response to nutrients, due to decreased root allocation (Brouwer 1962, Davidson 1969). Thus, these shifts in allocation by vascular plants, if they occurred, would have magnified all except the large nutrient responses we observed.

Initial (3-yr) changes in biomass were poor predictors of long-term changes because of lags in response by some species, different rates of response among species, compensatory responses among species, and feedbacks to nutrient and light availability by litter and shading, respectively. The immediate response to manipulation, approximated by our 3-yr measurements and other 1- and 2-yr studies (Chapin and Shaver 1985, Chapin et al. 1986, Shaver et al. 1986, Havström et al. 1993), is dominated by the direct growth response of individuals present at the beginning of the experiment. The 9-yr response more strongly reflects changes in growth, mortality, species competition, and feedbacks to resource availability. Even 1-yr responses of a subarctic tundra to elevated nutrients and temperature were poor predictors of 2-yr responses (Parsons et al. 1994). Other longer term responses, such as changes in soil properties and recruitment of new species, may further constrain the future response of tussock tundra to our manipulations and will strongly influence the longer term response of tundra to changes in climate (Hobbie et al. 1993).

Regional climatic warming during the past decade is more likely than autogenic vegetation succession to have caused the large vegetation change observed in our control plots. The large decline in biomass of *Eriophorum* in unmanipulated control plots during our 10-yr study is consistent with our manipulations simulating a warmer, more fertile environment and with decreased sedge pollen during warm periods of the Holocene (Ritchie and Cwynar 1982). Our study site has been deglaciated for at least 60 000 yr (Hamilton 1986, Walker et al. 1989) and dominated by tussock tundra for at least 7000 yr (Bergstrom 1984, Eisner 1991). We could find no charcoal in the 7000-yr peat profile, nor have there been any major herbivore outbreaks during the 16 yr we have worked at the site (Batzli and Henttonen 1990), suggesting that the vegetation is not changing rapidly in response to recent disturbances. By contrast, much of the Alaskan Arctic has shown a 4°C rise in permafrost temperature in the last 50 yr (Lachenbruch and Marshall 1986), with the decade of study having the warmest air temperatures on record (Trenberth 1990, Oechel et al. 1993). Similarly, there is a net annual CO_2 efflux from the study area (Oechel et al. 1993) equivalent in magnitude to NPP (Shaver and Chapin 1991) that has been ascribed to regional climatic warming and associated drying of soils.

Species diversity

The decline in species richness that we observed in response to nutrient addition is common (Mellinger and McNaughton 1975, Tilman 1982, but see Jonasson 1992). This reflects increased dominance of a few rapidly growing species and competitive elimination of understory taxa. Our 30–50% decline in species richness of tussock tundra after 9 yr suggests that the diversity of this ecosystem is also quite sensitive to treatments simulating climatic warming. Most concern about loss of species diversity with climate change has focused on the tropics (Solbrig 1991). However, because the tundra has so few species, any loss of species has a large proportional impact on tundra communities, perhaps leading to profound ecosystem consequences (Vitousek 1990). This is particularly important because of the large shifts in species abundance and loss of entire functional groups (lichens, mosses, and forbs) in the most extreme treatments. For example, inflorescences of the forb species, which disappeared or were strongly reduced in treatments simulating climatic warming, are nutritionally important and selectively grazed by caribou during lactation (White and Trudell 1980) and are the major plant species used by bumble bees and other pollinators (Williams and Batzli 1982). Lichens are critical to the over-winter nutrition of caribou (White and Trudell 1980), and mosses strongly influence soil thermal regime (Tenhunen et al. 1992). Thus, the loss of species diversity under climatic warming could have disproportionate effects on animal-mediated processes and on soil temperature.

Nutrient uptake

Tussock-tundra vegetation accumulated the N and P added as fertilizers much more efficiently (62 and 18%, respectively, of the amounts added in the first 3 yr) than do highly productive agricultural crops, reflecting the strong nutrient limitation typically found in vascular plants of tundra (Shaver and Chapin 1980) and the nearly complete cover of nonvascular plants, which

immediately absorbed the nutrients through direct contact. N was probably incorporated more efficiently than P into the vegetation for several reasons, including (1) N is the most limiting nutrient to plant growth at this site (Shaver et al. 1986), (2) P is more strongly retained in soils than is N (Black 1968), and (3) less N was applied relative to annual plant requirement (Shaver and Chapin 1991). The increase in nutrient uptake and turnover observed in the nutrient treatment is a typical response to improved soil fertility (Chapin 1980).

The fact that cations in vegetation increased in response to nutrient addition more strongly than biomass suggests that plants function to maintain relatively constant N:P:cation ratios, similar to marine algae (Redfield 1958), and that cations are relatively abundant (>98% base saturation) in soils of tussock tundra (Nadelhoffer et al. 1991). The increased cation uptake in the fertilized plots was presumably a consequence of greater sink strength associated with greater plant growth. Thus, patterns of nutrient uptake by plants are determined by both plant and soil processes, and are not a simple consequence of diffusion to the root surface, as previously assumed (Nye and Tinker 1977).

CONCLUSIONS

Our manipulations of temperature, nutrients, and light to simulate changes expected in the Arctic in the next 50–100 yr altered nutrient availability, growth-form composition, biomass, NPP, and species richness of tussock tundra in < a decade, due entirely to changes in relative dominance of resident species without immigration of new species. Thus, vegetation at this arctic site is quite sensitive to potential climatic warming. Observations of unmanipulated control plots suggest that similar vegetation changes may already be occurring in response to recent temperature increases in the Alaskan Arctic.

In general, only the responses to nutrients and light were predictable from a knowledge of growth form, suggesting that functional types can be defined with respect to their response to resources, but not their direct response to climate (Hobbie et al. 1993). As shown in our experiments and in the pollen record (COHMAP 1988), species responses to climatic changes are highly individualistic and not readily generalized. Thus, realistic predictions of the future distribution of vegetation with respect to climate must emphasize the indirect effects of climate on resource supply.

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