

Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra

M. SYNDONIA BRET-HARTE, ERICA A. GARCÍA, VINCIANE M. SACRÉ, JOSHUA R. WHORLEY, JOANNA L. WAGNER, SUZANNE C. LIPPERT and F. STUART CHAPIN III

Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA

Summary

1 Species interactions will probably be important in determining plant community structure as availability of soil nutrients changes due to climate warming or anthropogenic N deposition. We removed dominant species, combinations of species, and entire plant functional types, in fertilized and unfertilized plots in tussock tundra.

2 After 2 years, graminoids responded more strongly to fertilizer than other growth forms, and the responses of graminoids and deciduous shrubs to fertilizer were greater under neighbour removal than in the intact community. Deciduous shrubs, evergreen shrubs and graminoids increased their biomass with fertilization, whereas non-vascular plants decreased.

3 Dominant species from each growth form usually responded strongly to fertilization, but half of all subdominant species responded weakly or not at all. Few species responded to neighbour removal.

4 Soil nutrient availability, however, was elevated significantly by both fertilization and neighbour removal. Neighbour removal increased nutrient availability in fertilized plots by up to two orders of magnitude, and availability of NH_4^+ and NO_3^- in some unfertilized removal treatments was greater than in the fertilized intact community.

5 The failure of many plant species to respond with enhanced growth to soil nutrients made available by neighbour removal, despite their response to fertilization, could be due to (i) tundra plants having such rigid niche complementarity that they are unable to utilize these additional resources, or (ii) insufficient time having elapsed for the remaining species to respond, because nutrients derived from neighbour removal probably became available later than nutrients added as fertilizer.

6 There may be a high potential for loss of available nutrients from the tundra ecosystem when species composition changes, if the remaining plants cannot adjust to use nutrients made available by the loss of their neighbours.

Key-words: nitrogen, phosphorus, plant functional types, soil nutrient availability, species interactions

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Introduction

Human activities affect Earth's environment and ecosystems not only through direct impacts on climate and element cycling, but also by mediating extinctions and introductions of species (Sala *et al.* 2000). Species differ in traits that affect carbon and nutrient cycling rates, so the abundance and diversity of species must therefore affect ecosystem function. Differences among ecosystems in decomposition rate, for example, are sometimes determined more by species differences in

litter quality than by differences in climate (Flanagan & Van Cleve 1983). However, the extent to which species mediate an indirect ecosystem response to perturbation is still largely unknown.

Many terrestrial ecosystems are strongly nutrient-limited. However, the nitrogen fixed globally due to anthropogenic activities is now nearly twice that fixed by natural processes, and is expected to increase (Vitousek *et al.* 1997; Kaiser 2001). Nitrogen deposition already impacts many natural ecosystems (Holland *et al.* 1999). Where low temperature limits decomposition, climate warming will tend to increase soil nutrient availability still further (Chapin 1983; Giblin *et al.* 1991; Nadelhoffer *et al.* 1992; Harte *et al.* 1995).

Long-term experiments in Alaskan tussock tundra indicate that productivity is limited more by nutrient availability than by temperature or light availability (Chapin *et al.* 1995). Over a period of 15 years of fertilization with N and P, net primary productivity (NPP) and plant biomass increased, while community composition shifted from codominance by four different growth forms to dominance initially by graminoids (at 3 years), but ultimately by a single deciduous shrub, *Betula nana* (Chapin *et al.* 1995; Bret-Harte *et al.* 2001; Shaver *et al.* 2001), whose wood production was largely responsible for the increase in NPP (Bret-Harte *et al.* 2002; Shaver *et al.* 2001). In nearby dry heath tundra, fertilization caused smaller increases in productivity and led to dominance by the grass *Hierochloa alpina*, but caused no change in biomass relative to control after 8 years (Gough *et al.* 2002). Ecosystem capacity to respond to a perturbation such as fertilization may therefore depend on the characteristics of the species that becomes dominant (also see Gough *et al.* 2000).

Since 1997, we have been investigating how species traits and diversity affect ecosystem processing of C and N in tussock tundra at Toolik Lake, by means of a field experiment removing different combinations of species and functional types, with or without fertilization. The usefulness and limitations of removal experiments have been reviewed recently (Diaz *et al.* 2003). We wished to answer two questions. First, to what extent do species interactions affect the trajectory of community and ecosystem response to environmental perturbation? Secondly, to what extent does ecosystem capacity to respond to perturbation depend on species identity? Tundra plants may have achieved coexistence through niche differentiation to partition soil nitrogen (McKane *et al.* 2002). We hypothesized that alleviation of nutrient limitation could allow light to become limiting, and species interactions therefore to become more important, after fertilization. If species' fundamental and realized niches were not the same, we hypothesized that initial removal effects would be mediated through increased soil nutrient availability to remaining members of the community, and that graminoids, which showed the strongest response to fertilization initially (Chapin *et al.* 1995), would be most affected.

We report the transient response of plants and soil to neighbour removal and fertilization here. Subsequent ecosystem retention of nutrients and the trajectory of vegetation development can be strongly affected by the dynamics of plant and soil responses in the first few years after a perturbation. Both transient and long-term measurements are needed to fully understand ecosystem response.

After consideration of plant characteristics traits that affect rates of nutrient cycling and carbon storage, such as stature, litter decomposability and thermal insulation, it was proposed that physiognomic growth forms (deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses and lichens) also describe species' functional roles in tussock tundra (Chapin *et al.* 1996). We tested

this classification by removing single species, pairs of species from different functional types, or all members of a functional type (deciduous shrubs or mosses). Because plant stature is thought to be an important factor affecting C storage (Chapin *et al.* 1996), and because evergreen shrubs and deciduous shrubs include species that are both tall and short, we addressed the issue of stature directly, by removing all canopy shrubs. We did not manipulate graminoids, because the most common graminoid species, *Eriophorum vaginatum*, is a tussock-forming sedge on which many other species grow. Removing tussocks would create a large disturbance and change the microtopography. We hope to see whether remaining members of the same functional type compensate more for a given species' absence than do members of other functional types (Walker *et al.* 1999). Because we are testing whether different members of a growth form are functionally similar, we refer to these groups as growth forms rather than functional types when describing their biomass response.

Materials and methods

SITE DESCRIPTION AND EXPERIMENTAL TREATMENTS

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

In 1997, we established six replicate blocks in homogeneous acidic tussock tundra on a gentle (5%) north-facing slope, approximately 100 m uphill from the LTER experimental plots (Bret-Harte *et al.* 2001, 2002) on the same geological surface. Each block consisted of a row of 2 × 3 m plots, 17 in all, with each plot separated from adjacent plots by 1-m buffer strips. Blocks were orientated perpendicular to the slope, separated from each other by 2-m buffer strips. Boardwalks, slightly elevated on wooden piers, were constructed in the 1-m buffer strips between the plots and around the perimeter of the experiment, so plots could be accessed without trampling. Within each block, seven plots were randomly assigned to treatments involving removal of single dominant species or groups of species from the same or different functional types (Table 1). An additional seven plots were randomly assigned to receive the same species removal treatments specified above, plus N and P fertilizers. The remaining three plots in

Table 1 Neighbour removal treatments. All these treatments were done both in the absence (letter code) and in the presence of N + P fertilization (letter code followed by 'F')

| Treatment code | Species removed | Reason for removal | Functional type |
|----------------|---|---|--|
| B, BF | <i>Betula nana</i> | Most common deciduous shrub, becomes dominant over the long term in fertilized tussock tundra | Deciduous shrub |
| L, LF | <i>Ledum palustre</i> | Most common evergreen shrub, the only evergreen in the canopy | Evergreen shrub |
| T, TF | <i>B. nana</i> , <i>L. palustre</i> | Most common members of two different functional groups | |
| M, MF | All moss species | Mosses insulate soil, contribute to peat formation and slow N cycling | Mosses |
| Z, ZF | All mosses, <i>B. nana</i> , <i>L. palustre</i> | Most common members of three different functional groups | |
| P, PF | <i>B. nana</i> , <i>L. palustre</i> , <i>Vaccinium uliginosum</i> , <i>Salix pulchra</i> | All those shrubs that can form a tall canopy | Canopy shrubs (alternate classification) |
| D, DF | <i>B. nana</i> , <i>Arctostaphylos alpina</i> , <i>V. uliginosum</i> , <i>S. pulchra</i> , <i>Rubus chamaemorus</i> | All common deciduous shrubs, which have the most decomposable leaf litter | Deciduous shrubs |
| C, U, F | None | Disturbed control (C), undisturbed control (U), and disturbed fertilized (F) treatments | |

each block were randomly assigned to treatments that did not involve any species removals: disturbed control (C), undisturbed control (U), and fertilizer addition (F) (see below).

In the removal treatments, vascular plant target species were removed by pulling out the above-ground stems and as much as possible of the below-ground stems until they broke below ground. Care was taken to avoid breaking the stems of non-target species, but some damage did occur, particularly to fine roots of species next to stems of the target species. Mosses were removed by pulling up the green moss and any attached brown tissue. Dead moss was left in place, and we returned most lichens removed with moss to the plot. C and F plots were disturbed to simulate the physical effects of removal by pulling on the stems of the vegetation without breaking them and by disrupting the moss layer by grabbing and shaking it. No biomass was removed from C, F or U plots. After establishment of the removal treatments in 1997, some below-ground stem material remained, and regrowth occurred. Treatments were maintained by removing the regrowth of target species, removing any recolonizing mosses, and by disturbing the C and F plots, in early June and late July 1998, and in early June 1999. The biomass of each species removed from the plots was dried for 72 h at 65 °C and weighed (Table 2).

For all fertilization treatments, we applied N and P fertilizers at the same rates and using the same application methods as in previous work (Shaver & Chapin 1980; Shaver & Chapin 1986; Chapin *et al.* 1995; Chapin & Shaver 1996; Bret-Harte *et al.* 2001). N and P were

Table 2 Total plant biomass removed from treated plots from 1997 to 1999, including regrowth

| Removal treatment | Biomass (g m ⁻²) | | |
|-------------------|------------------------------|------------|------------|
| | Vascular plants | Mosses | Total |
| B | 127 (7.0) | 0 (0) | 127 (7.0) |
| BF | 124 (22.9) | 0 (0) | 124 (22.9) |
| L | 209 (28.5) | 0 (0) | 209 (28.5) |
| LF | 179 (17.4) | 0 (0) | 179 (17.4) |
| T | 320 (12.9) | 0 (0) | 320 (12.9) |
| TF | 382 (23.0) | 0 (0) | 382 (23.0) |
| M | 0 (0) | 638 (56.1) | 638 (56.1) |
| MF | 0 (0) | 610 (73.6) | 610 (73.6) |
| Z | 379 (24.7) | 719 (101) | 1098 (111) |
| ZF | 407 (37.9) | 842 (94.2) | 1249 (115) |
| P | 390 (18.6) | 0 (0) | 390 (18.6) |
| PF | 334 (17.0) | 0 (0) | 334 (17.0) |
| D | 169 (16.8) | 0 (0) | 169 (16.8) |
| DF | 162 (11.2) | 0 (0) | 162 (11.3) |

Means are reported, with 1 SE in parentheses ($n = 6$ blocks). No biomass was removed from the control (C), fertilized (F), and undisturbed control (U) plots. Treatment abbreviations are as listed in Table 1.

applied annually in early June, starting in 1997. We applied N (as slow-release granular NH_4NO_3) at $10 \text{ g N m}^{-2} \text{ y}^{-1}$ and P (as commercial granular superphosphate, a mixture of calcium phosphates) at $5 \text{ g P m}^{-2} \text{ y}^{-1}$. These rates are higher than natural inputs of nutrients (about four times the annual N requirement and 20 times the annual P requirement of the vascular plants; Shaver & Chapin 1991). Our intent was not to simulate a particular scenario of N deposition under climate change, but rather to see

effects of altered species composition in an ecosystem relieved of nutrient limitation.

ENVIRONMENTAL MONITORING

We measured soil temperature at 5 cm below the moss or soil surface in intertussock areas using copper-constantan thermocouples (Omega Engineering Incorporated, Stamford, Connecticut, USA) in three plots of each of the following treatments: C, F, M, MF, B, BF, L, LF, Z, ZF (Table 1). Values were continuously recorded with a datalogger (CR10; Campbell Scientific Incorporated, Logan, Utah, USA), starting in 1997. Measurements were made every 5 min, with 3-hourly averages recorded. We also recorded spot measurements of soil temperatures at 5 and 12 cm below the surface at four locations in each plot of all treatments over the course of 3 days in late July 1999. We recorded thaw depth at four locations in each plot on 18 August 1997 and 9 August 1999, by pushing a thin metal probe from the moss surface to the bottom of the thawed soil in intertussock areas. Wind speed and direction, air temperature, relative humidity and light intensity are measured by the Arctic LTER (Bret-Harte *et al.* 2001) 100 m from our plots, and are available at <http://ecosystems.mbl.edu/arc/home.htm>.

ESTIMATION OF ABOVE-GROUND BIOMASS

We collected data on initial biomass of all vascular and non-vascular plants in five of six blocks immediately following species removal in 1997, and again in the same locations plus the sixth block in 1999, via non-destructive point-intercept sampling (Jonasson 1988; Hobbie *et al.* 1999; Shaver *et al.* 2001). In each plot, a randomly chosen 75 × 75 cm subplot with corners at least 20 cm from the plot edge was selected, excluding non-vegetated frost boils. In this subplot, repeated hits of vegetation by a metal rod (5 mm = 3/16 inch diameter) were recorded by species and tissue type, from the top of the canopy to the soil or moss surface, at 100 equally spaced points. Above-ground biomass was estimated from the number of hits using regression relationships developed previously from point-intercept sampling on quadrats that were subsequently harvested by clipping all above-ground biomass (Shaver *et al.* 2001). Regressions had the best explanatory power at the level of functional groups (Shaver *et al.* 2001). For this analysis, those regressions were recalculated forcing the intercept through zero (Hobbie *et al.* 1999). Biomass (g m⁻²) equals hits per pin multiplied by 1.88833 (deciduous shrubs), 0.66658 (evergreen shrubs), 0.36800 (graminoids), 0.16123 (forbs), 1.42068 (moss), or 1.00370 (lichens).

SHOOT TYPE DETERMINATION IN *BETULA NANA*

Betula nana has long/short shoot dimorphism (Bret-Harte *et al.* 2001). In late July of 1999, the proportion of long

and short shoots in the most apical 10 shoots was measured on 10 randomly selected ramets (large, rooted branches) of *Betula nana* in each plot where it occurred.

SOIL NUTRIENT AVAILABILITY

We measured the accumulation of NH₄⁺, NO₃⁻ and PO₄⁻ on ion exchange resins incubated in the soil to compare the relative availability of N and P in the different treatments (Giblin *et al.* 1991). Resin bags made of nylon stocking material were soaked in 0.1 M HCl overnight before filling with ion exchange resins. Each bag contained 9 g FW of mixed-bed ion exchange resins (IONAC® nm-60 H⁺/OH⁻ form, type I beads 16–50 mesh; J.T. Baker, Phillipsburg, New Jersey, USA). Resin bags (one per plot) were placed at approximately 5 cm depth in the soil on 22 June and were removed on 14 August 1999. Resin bags were washed free of soil using distilled water, then extracted in 100 mL 2 M NaCl in 0.1 M HCl overnight. Extracts were frozen until analysis. Several samples were lost prior to analysis, but at least four replicates were analysed per treatment. For analysis, extracts were thawed in a refrigerator, then brought to neutral pH by the addition of NaOH, and analysed colourimetrically for NH₄⁺, NO₃⁻ and PO₄⁻ (Whitledge *et al.* 1981) on a modified Technicon autoanalyser (Tarrytown, New York, USA).

STATISTICAL ANALYSES

Point-intercept data for each species were initially analysed by repeated measures ANOVA (GLM with block, fertilization, neighbour removal and a fertilization by neighbour removal interaction as between subject effects, and time, time by fertilization interaction, time by neighbour removal and time by fertilization by neighbour removal interactions as within subject effects; JMP Statistical Software). For each species, treatments from which that species was removed were excluded from the analysis. All data were tested for homogeneity of variance (Cochran's *C*-test; Winer *et al.* 1991) prior to analysis. If necessary, data were transformed using the algorithm $y = \ln(x + 1)$ (Zar 1999).

In virtually all analyses, the effect of time was significant and there was often a significant time by fertilization interaction. Accordingly, point-intercept data from each year were analysed separately by ANOVA, using a GLM with block, fertilization and neighbour removal treatment as main effects, and a fertilization by removal interaction term. Results of 1999 analyses are presented here. Point-intercept data were also analysed by lumping together members of each growth form, using the same GLM model specified above, and including only treatments from which members of that growth form were not removed.

Soil nutrient data, which were collected only in 1999, were analysed by ANOVA (GLM with block, fertilization and neighbour removal as main effects, and a fertilization by neighbour removal interaction term). Because

of high variance in the fertilized treatments, the PO_4^- data had inhomogeneous variance even after transformation; these data were ranked, and ANOVA (same model as above) was conducted on the ranks (Zar 1999). This non-parametric test gave the same qualitative results as the parametric ANOVA, suggesting that the non-parametric test had sufficient power to detect differences (Zar 1999). Data on soil temperatures and depth of thaw were analysed using the same model for each year and/or depth of measurement separately.

For each variable measured, data from the disturbed control treatment and the undisturbed control treatment were compared using *t*-tests. There was never a significant difference between data from disturbed and undisturbed control treatments; thus the disturbed control was used in all ANOVAs.

Because the amount of biomass removed was not randomly distributed across the treatments, it could not be used as a covariate in ANCOVA. To understand how important the amount of biomass removed was to predicting the biomass response of remaining plants or soil nutrient availability in 1999, we used multiple regression. We regressed either point-intercept hits for each growth form, or nutrient availability, against biomass removed between 1997 and 1999, point-intercept hits in 1997 and categorical factors representing neighbour removal and fertilization. We expected that changes in remaining plant biomass in response to neighbour removal would be fairly small compared with original biomass, at least for common species, so that biomass in 1997 would predict biomass in 1999. Categorical factors for neighbour removal included removal of *Ledum*, removal of *Betula*, removal of moss, removal of all canopy shrubs, and removal of all deciduous shrubs. These factors applied to all treatments that included that removal, so, for example, the M, MF, Z and ZF treatments had the same value for the variable 'removal of moss'. Categorical factors were the same for soil nutrient data, but we did not include 1997 biomass. We generated models with all possible combinations of these factors, then used the modified Akaike's information criterion (AIC_c) to select the models that best predicted either biomass for each growth form or nutrient availability in 1999 (Akaike 1973; Anderson *et al.* 2000). The AIC_c allows selection of the best model for a set of data given an *a priori* set of alternative hypotheses, rather than testing a null hypothesis (Anderson *et al.* 2000).

Results

Neighbour removal treatments differed in the amount of above- and below-ground biomass removed between 1997 and 1999 (Table 2). Removing moss, *Betula* and *Ledum* together (Z and ZF) took out the most biomass, while removing *Betula* alone (B and BF) took out the least biomass, only one-tenth as much (Table 2). Removing moss alone (M and MF) took out nearly twice as much biomass as any removal treatment involving only vascular plants (Table 2). (Because we removed the

green parts of the moss and any attached brown tissue, our removed moss biomass is greater than the green moss biomass measured in previous studies (Shaver & Chapin 1991).) Of the total cumulative plant biomass removed, an average of 70% was removed in 1997 when the experiment was established; 17% was removed in 1998 and 13% in 1999 because of regrowth from surviving underground stems and brown, but live, moss bodies, or colonization by mosses from spores.

ABOVE-GROUND PLANT BIOMASS

Estimated above-ground biomass of all vascular plants was approximately twice that of all non-vascular plants (Fig. 1a,b). Estimated biomass of vascular plants in all plots was higher in 1999 than in 1997 (Fig. 1a). Estimated biomass of non-vascular plants in 1999 was higher than in 1997 in unfertilized plots, but generally decreased in fertilized plots (Fig. 1b). Control plots had 15–20% more biomass in 1999 than in 1997 (Fig. 1), which could reflect either the favourable climate in 1998 and 1999, or differences in point-frame technique between data collectors in 1997 and 1999. The change in control plots between 1997 and 1999 is within the range of year-to-year variability previously observed in control tussock tundra at Toolik Lake (Shaver *et al.* 2001).

Evergreen shrubs had the greatest biomass of any growth form in control plots, but this was only slightly

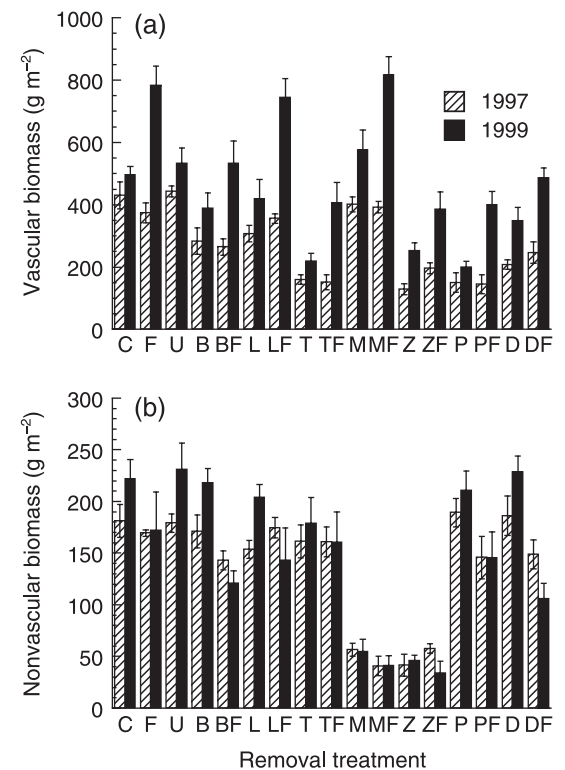


Fig. 1 Total above-ground plant biomass in 1997 and 1999, as estimated from point-intercept sampling. Abbreviations for neighbour removal treatment are given in Table 1. (a) Vascular plants, (b) non-vascular plants. Error bars indicate 1 SE, for $n =$ six blocks.

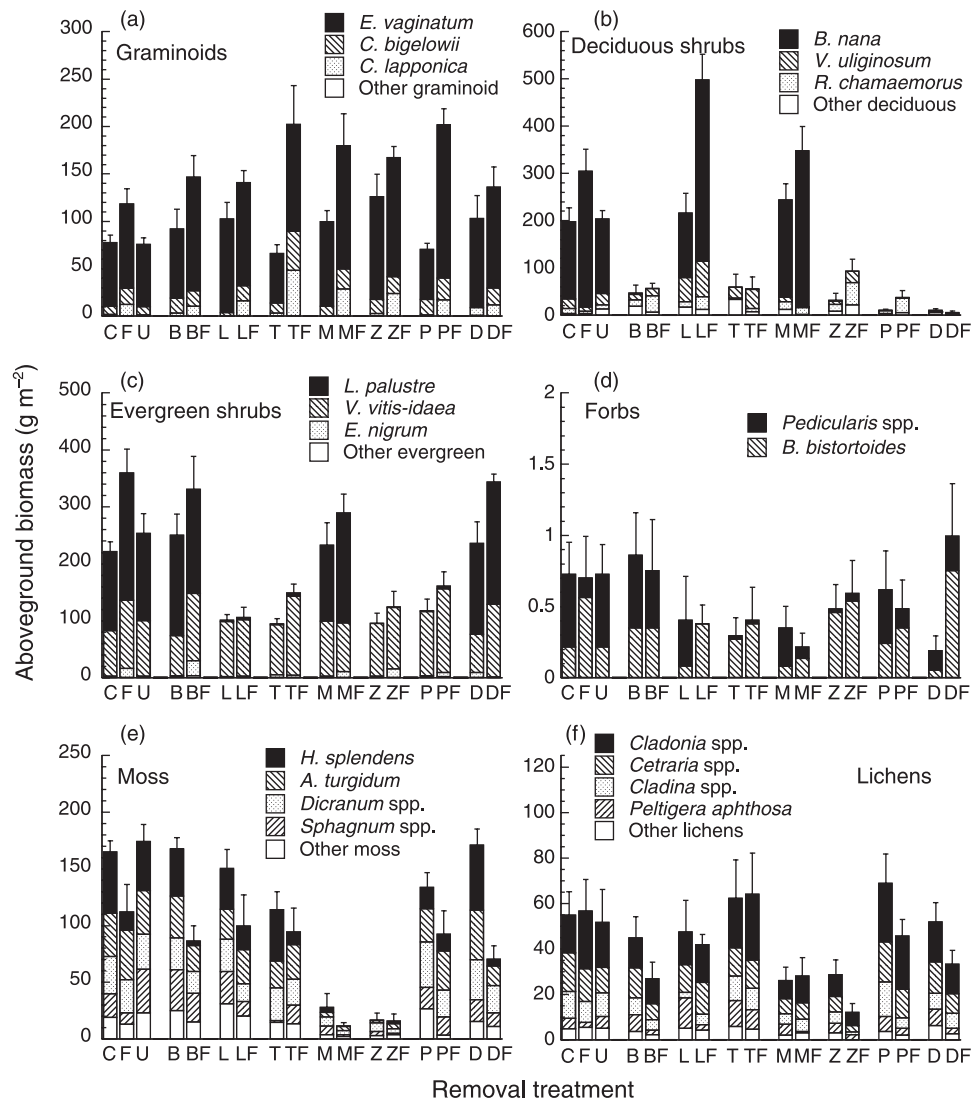


Fig. 2 Estimated above-ground biomass in 1999 of the major growth forms of plants, with the three to four most common species indicated for each growth form. The species with the most biomass in each growth form under control conditions is shown first (black bars). Non-vascular plants were mostly identified to genus. Abbreviations for neighbour removal treatments are given in Table 1. Full species names are as follows. Graminoids: *Eriophorum vaginatum*, *Carex bigelowii*, *Calamagrostis lapponica*, 'other graminoid' is mainly composed of *Luzula confusa* and *Heirochloa alpina*. Deciduous shrubs: *Betula nana*, *Vaccinium uliginosum*, *Rubus chamaemorus*, 'other deciduous' is mainly composed of *Arctostaphylos alpina*, *Salix pulchra* and *Salix phlebophylla*. Evergreen shrubs: *Ledum palustre*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, 'other evergreen' is mainly *Cassiope tetragona*. Forbs: *Pedicularis* spp. (mainly *Pedicularis lapponica*; several species of *Pedicularis* did not flower, so could not be identified), *Bistorta bistortoides*, no other forbs were encountered. Moss: *Hylocomium splendens*, *Aulacomnium turgidum*, 'other moss' is mainly *Rhytidium rugosum*, *Drepanocladus* spp. and unidentified liverworts. Lichens: *Peltigera aphthosa*, 'other lichens' includes mainly *Thamnolia* spp., with some *Masonhalla richardsonii*. Error bars indicate 1 SE for the entire growth form ($n = 6$ blocks).

greater than that of deciduous shrubs or mosses (Fig. 2). Despite the visual prominence of *Eriophorum vaginatum* in tussock tundra, graminoids and lichens had less biomass than shrubs or mosses, and forbs were rare (Fig. 2). In 1999, all growth forms except forbs showed significant effects of fertilization (Table 3). For mosses and lichens, fertilization caused a significant decrease in biomass, while fertilization significantly increased the biomass of graminoids, deciduous shrubs and evergreen shrubs (Fig. 2).

Both graminoids and deciduous shrubs showed marginally significant, synergistic, neighbour removal by fertilization interaction effects in 1999 (Table 3).

Graminoids responded to fertilizer more strongly in removal treatments than in the intact community in 1999, but not in 1997. Deciduous shrubs showed a significant neighbour removal by fertilization immediately following initial removal treatment (1997 ANOVA statistics not shown), because *Ledum* removal increased deciduous shrub biomass under fertilization in both 1997 and 1999. This suggested that the effect of removing *Ledum* under fertilization might have been partly caused by initial differences in species composition between plots. However, the difference between deciduous shrubs in F and LF plots was greater in 1999 than in 1997 (194 g m⁻² in 1999, 100 g m⁻² in 1997), suggesting that *Ledum* removal

Table 3 Results of 1999 ANOVAs on estimated biomass of entire growth forms, including only those treatments where members of that growth form were not intentionally removed. Nd.f. = numerator degrees of freedom, Dd.f. = denominator degrees of freedom, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.1$, NS = non-significant

| Growth form | Factor | | | | | | | | | | | |
|------------------|--------|-------|-----------|------------------------|-------|-----------|--------------------|-------|-----------|---------|-------|----------|
| | Block | | | Neighbour removal (NR) | | | Fertilization (Ft) | | | NR × Ft | | |
| | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> |
| Deciduous shrubs | 5 | 25 | 1.256 NS | 2 | 25 | 2.998† | 1 | 25 | 21.369*** | 2 | 25 | 2.752† |
| Evergreen shrubs | 5 | 35 | 1.158 NS | 3 | 35 | 0.313 NS | 1 | 35 | 13.242*** | 3 | 35 | 0.448 NS |
| Graminoids§ | 5 | 75 | 0.3186 NS | 7 | 75 | 1.2104 NS | 1 | 75 | 56.963*** | 7 | 75 | 1.978† |
| Forbs§ | 5 | 75 | 1.933 NS | 7 | 75 | 1.326 NS | 1 | 75 | 0.224 NS | 7 | 75 | 0.988 NS |
| Mosses | 5 | 55 | 2.670* | 5 | 55 | 0.911 NS | 1 | 55 | 33.346*** | 5 | 55 | 1.390 NS |
| Lichens | 5 | 75 | 3.874** | 7 | 75 | 4.808*** | 1 | 75 | 3.862* | 7 | 75 | 0.600 NS |

§Data were ln-transformed to achieve homogeneity of variance.

under fertilization increased deciduous shrub biomass over time. Lichens declined significantly under neighbour removal (Table 3) because lichen abundance decreased in all treatments involving moss removal, as well as the *Betula* removal treatment, in both 1999 and 1997. This probably occurred because we could not remove moss without also removing some lichens, despite our efforts to avoid this.

A key question in understanding the link between diversity and ecosystem function concerns the role of the amount of plant biomass vs. the identity of that biomass (Díaz *et al.* 2003). Because plant density cannot be controlled in a removal experiment, it is important to assess the extent to which results may be a function of the amount of biomass removed. Multiple regression models indicated that, although the amount of biomass removed sometimes affected the response of remaining plant biomass to the experimental treatments, it was not the most important factor. The best regression models for the response of biomass of each particular growth form, according to the AIC_c criterion, explained 40–50% of the variation in the respective data sets, except for forbs (34%) and deciduous shrubs (75%). Initial point-frame hits in 1997 occurred in the best models for all growth forms. Fertilization occurred in the best models for every growth form except forbs, and was the single most important predictive factor, by itself explaining 30–40% of the variance in those data sets. In contrast, the amount of biomass removed occurred in the best models for only half the growth forms (graminoids, mosses and deciduous shrubs) and, by itself, never explained more than 10% of the variance in any data set.

ABOVE-GROUND BIOMASS OF SPECIES

Species responded individualistically to removals and fertilization, and not all the species within a growth form responded in the same manner (Table 4, Fig. 2). In 1999, fertilization had strong effects on the species with the greatest biomass (hereafter called the dominant) in each growth form except forbs and lichens (Fig. 2,

Table 4). Fertilization strongly increased the biomass of the dominant vascular species (*Betula nana*, *Ledum palustre* and *Eriophorum vaginatum*), but decreased that of the dominant moss (*Hylocomium splendens*) (Fig. 2, Table 4). Dominant species made up 30–86% of the biomass of their respective growth forms in control plots, with the greatest evenness in non-vascular growth forms, and the strongest dominance in graminoids (*E. vaginatum*) and deciduous shrubs (*B. nana*) (Fig. 2).

Fertilization sometimes increased the biomass of subdominant members of each growth form. One of the strongest fertilization responses was observed in the subdominant graminoid *Calamagrostis lapponica*, which could not be detected in the plots in 1997, but by 1999 had become a significant component of graminoid biomass in fertilized removal plots, especially fertilized *Betula* + *Ledum* removal plots (TF plots, Fig. 2, Table 4). Other subdominant species that responded strongly to fertilization in 1999 included the evergreen shrub *Vaccinium vitis-idaea* and the N-fixing lichen *Peltigera aphthosa*, which was the only lichen to respond negatively to fertilizer (Fig. 2, Table 4), but half of the common subdominant species did not respond significantly to fertilization at the $P < 0.05$ level (Table 4).

Generally, it was the subdominants within each growth form except forbs and lichens that showed significant effects of neighbour removal in 1999 (e.g. *Vaccinium uliginosum*, *Carex bigelowii* and *Sphagnum* spp., Table 4). However, for all of these species, the same removal treatments were also significantly different from controls in 1997 (ANOVA statistics not shown), at which time plants would have only part of one growing season to respond to neighbour removal. This suggests that initial differences in plant distribution among plots are a more likely explanation for these removal effects. In contrast, the dominant forb, *Pedicularis* spp., showed a significant neighbour removal effect in 1999 (but not 1997), which was caused by significant declines under treatments involving the removal of *Ledum* (Table 4).

Increased long shoot production in *B. nana* was not observed prior to 1999, when both fertilization and, to

Table 4 Results of species-level analysis of variance on 1999 point-frame hits for all species and on frequency of long shoots in ramets of *Betula nana*. Treatments analysed included only those from which the given species was not removed. Abbreviations as in Table 3

| Growth form <i>Species</i> | Factor | | | | | | | | | | | |
|----------------------------------|--------|-------|----------|------------------------|-------|-----------|--------------------|-------|-----------|---------|-------|----------|
| | Block | | | Neighbour removal (NR) | | | Fertilization (Ft) | | | NR × Ft | | |
| | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> | Nd.f. | Dd.f. | <i>F</i> |
| Deciduous shrubs | | | | | | | | | | | | |
| <i>Betula nana</i> | 5 | 25 | 0.744 NS | 2 | 35 | 0.620 NS | 1 | 25 | 24.814*** | 2 | 25 | 1.498 NS |
| <i>B. nana</i> long shoots | 5 | 349 | 1.860 NS | 2 | 349 | 10.279*** | 1 | 349 | 1149.5*** | 2 | 349 | 0.312 NS |
| <i>Vaccinium uliginosum</i> § | 5 | 55 | 3.589** | 5 | 55 | 2.027† | 1 | 55 | 0.010 NS | 5 | 55 | 0.444 NS |
| <i>Rubus chamaemorus</i> § | 5 | 65 | 9.423*** | 6 | 65 | 1.092 NS | 1 | 65 | 3.543† | 6 | 65 | 1.020 NS |
| Evergreen shrubs | | | | | | | | | | | | |
| <i>Ledum palustre</i> | 5 | 35 | 1.116 NS | 3 | 35 | 0.320 NS | 1 | 35 | 7.698** | 3 | 35 | 0.776 NS |
| <i>Vaccinium vitis-idaea</i> | 5 | 75 | 0.866 NS | 7 | 75 | 1.174 NS | 1 | 75 | 13.101*** | 7 | 75 | 1.145 NS |
| <i>Empetrum nigrum</i> § | 5 | 75 | 0.150 NS | 7 | 75 | 0.553 NS | 1 | 75 | 0.726 NS | 7 | 75 | 1.488 NS |
| Graminoid | | | | | | | | | | | | |
| <i>Eriophorum vaginatum</i> | 5 | 75 | 0.897 NS | 7 | 75 | 0.799 NS | 1 | 75 | 14.372*** | 7 | 75 | 1.226 NS |
| <i>Carex bigelowii</i> § | 5 | 75 | 2.082† | 7 | 75 | 2.722* | 1 | 75 | 9.202** | 7 | 75 | 1.201 NS |
| <i>Calamagrostis lapponica</i> § | 5 | 75 | 1.458 NS | 7 | 75 | 1.362 NS | 1 | 75 | 57.792*** | 7 | 75 | 1.226 NS |
| Forbs | | | | | | | | | | | | |
| <i>Pedicularis</i> spp.§ | 5 | 75 | 2.836* | 7 | 75 | 2.359* | 1 | 75 | 2.708 NS | 7 | 75 | 0.630 NS |
| <i>Bistorta bistortoides</i> § | 5 | 75 | 0.717 NS | 7 | 75 | 1.187 NS | 1 | 75 | 3.316† | 7 | 75 | 0.801 NS |
| Mosses | | | | | | | | | | | | |
| <i>Hylocomium splendens</i> § | 5 | 55 | 0.945 NS | 5 | 55 | 1.664 NS | 1 | 55 | 56.086*** | 5 | 55 | 4.468** |
| <i>Aulacomnium turgidum</i> § | 5 | 55 | 1.061 NS | 5 | 55 | 1.283 NS | 1 | 55 | 1.274 NS | 5 | 55 | 1.907 NS |
| <i>Dicranum</i> spp.§ | 5 | 55 | 2.728* | 5 | 55 | 1.095 NS | 1 | 55 | 8.798** | 5 | 55 | 0.713 NS |
| <i>Sphagnum</i> spp. | 5 | 55 | 2.442* | 5 | 55 | 1.981† | 1 | 55 | 1.650 NS | 5 | 55 | 1.117 NS |
| Lichens | | | | | | | | | | | | |
| <i>Cladonia</i> spp. | 5 | 75 | 3.767** | 7 | 75 | 4.729*** | 1 | 75 | 0.274 NS | 7 | 75 | 0.706 NS |
| <i>Cetraria</i> spp. | 5 | 75 | 2.123† | 7 | 75 | 6.017*** | 1 | 75 | 5.6215* | 7 | 75 | 0.912 NS |
| <i>Cladina</i> spp.§ | 5 | 75 | 2.375* | 7 | 75 | 3.791** | 1 | 75 | 2.744 NS | 7 | 75 | 1.398 NS |
| <i>Peltigera aphthosa</i> § | 5 | 75 | 1.839 NS | 7 | 75 | 2.500* | 1 | 75 | 17.686*** | 7 | 75 | 0.646 NS |
| <i>Thamnia</i> spp.§ | 5 | 75 | 0.710 NS | 7 | 75 | 1.018 NS | 1 | 75 | 2.391 NS | 7 | 75 | 0.498 NS |

§Data were ln-transformed to achieve homogeneity of variance.

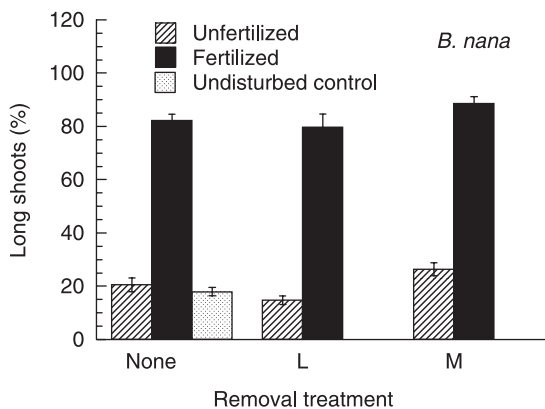


Fig. 3 The proportion of long shoots in the 10 most apical shoots of ramets of *Betula nana* in 1999. Abbreviations for neighbour removal treatments are in Table 1, error bars indicate 1 SE, $n = 6$ blocks.

a lesser extent, moss removal significantly increased long shoot frequency (Fig. 3, Table 4).

Because plant responses to neighbour removal were so minimal, we could not determine from these data whether the ecological function of a removed species is

compensated for by members of the same or different functional types (Chapin *et al.* 1996).

SOIL NUTRIENT AVAILABILITY

In both disturbed and undisturbed control plots, nitrogen availability (NO_3^- and NH_4^+), as measured by accumulation on ion exchange resins, was low, with approximately an order of magnitude less NO_3^- than NH_4^+ (Fig. 4). PO_4^- availability was also very low (Fig. 4). In contrast to the minimal effects of neighbour removal on plant species, both neighbour removal and fertilization caused highly significant increases in relative nutrient availability in the soil (Fig. 4, Table 5). For NH_4^+ , there was also a significant, synergistic neighbour removal by fertilization interaction (Table 5), because neighbour removal increased NH_4^+ availability much more in fertilized than in unfertilized plots. Available N and P increased by nearly three orders of magnitude in some fertilized removal plots, although increases under fertilization without neighbour removal were much smaller (Fig. 4). Fertilization also increased the relative proportion of N as NO_3^- (Fig. 4). The highest recorded

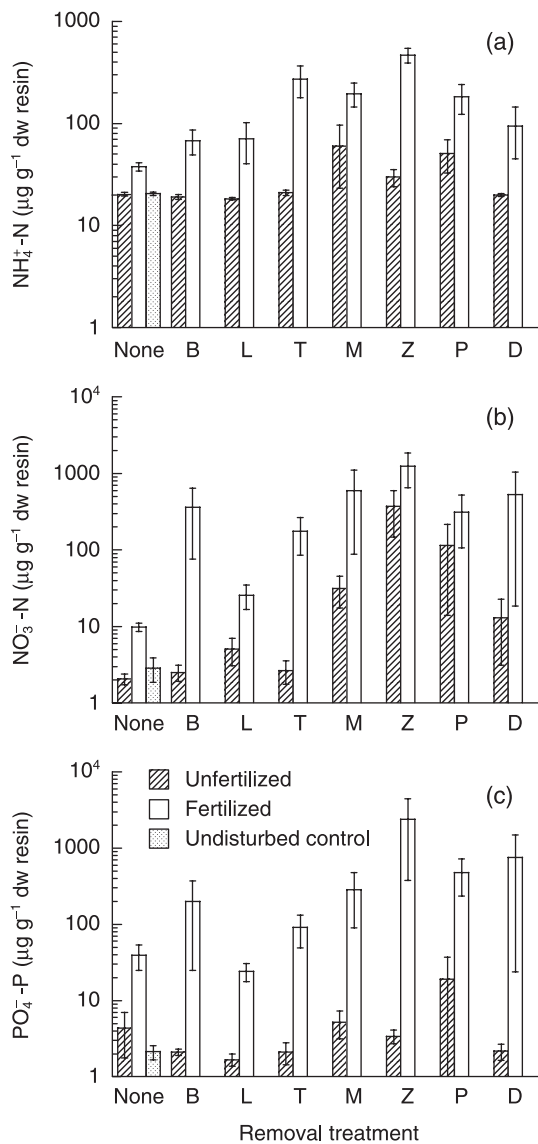


Fig. 4 Soil nutrient availability in 1999, as measured by accumulation on ion exchange resins. (a) the mass of N present as NH_4^+ ; (b) the mass of N present as NO_3^- ; (c) the mass of P present as PO_4^- . Note the logarithmic scale on the y-axis. Abbreviations for neighbour removal treatments are given in Table 1. Error bars indicate 1 SE, $n = 4-6$, depending on treatment.

values of both anions and cations were lower than the ion exchange capacity of the resin bags.

Neighbour removal significantly increased relative soil nutrient availability of both nitrogen species under treatments that removed (i) mosses alone, (ii) *Betula* and *Ledum*, (iii) moss, *Betula* and *Ledum*, and (iv) all canopy shrubs. These four removal treatments took away the most biomass (Table 2), and had the highest graminoid biomass, particularly when fertilized (Fig. 3). For PO_4^- , neighbour removal increased soil nutrient availability under removal of (i) moss, *Betula* and *Ledum*, and (ii) all canopy shrubs.

Multiple regression models indicated that, though the amount of biomass removed sometimes affected nutrient availability under the experimental treatments, it was

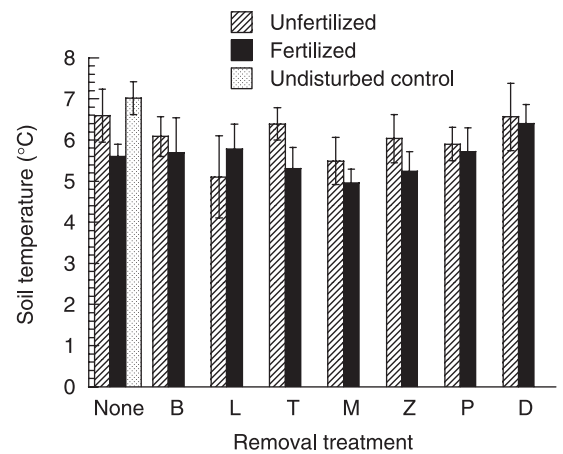


Fig. 5 Soil temperature at 5 cm depth, measured from 27 to 29 July 1999. Abbreviations for neighbour removal treatments given in Table 1. Error bars indicate 1 SE, $n = 6$ blocks.

not as important as the type of biomass removed. The best regression models for nutrient availability, according to the AIC_c criterion, explained 50–66% of the variation in the nutrient availability data. Fertilization was the most important factor in the best models for all three ions, by itself explaining 46% (NH_4^+), 27% (NO_3^-) and 60% (PO_4^-) of the variation. The amount of biomass removed was a factor only in the best model for NH_4^+ availability, by itself explaining 11% of the variation, while moss removal was a factor in the best models for both NO_3^- and PO_4^- , by itself explaining 17% (NO_3^-) and 2% (PO_4^-) of the variation.

SOIL TEMPERATURE AND THAW DEPTH

Neighbour removal did not significantly affect soil temperature in spot measurements at 5 cm or 12 cm depth in 1999. Fertilization reduced soil temperature at 5 cm (Fig. 5, Table 5), but not 12 cm depth. Although there were clear seasonal patterns in soil temperature in continuously instrumented plots, there were no significant differences between neighbour removal or fertilization treatments in 1999 or 1997 (data not shown). Fertilization and neighbour removal did not affect depth of thaw, which provides an integrated measure of soil temperature over the growing season, in either 1999 (Table 5) or 1997 (data not shown).

Discussion

Some plant species, particularly dominants, showed substantial changes in biomass in response to fertilizer after 2 years, but others did not; thus, members of the same growth form did not respond equally or in the same way. This agrees with previous observations that growth forms do not differ consistently in the response of their growth (Chapin & Shaver 1985), or of their nutrient and total non-structural carbohydrate concentrations, to fertilization (Shaver & Chapin 1980). However, all significant responses of vascular plants to fertilizer were

Table 5 Results of analysis of variance on relative nutrient availability in the soil as measured by accumulation on ion exchange resins, soil temperature at 5 cm depth in late July 1999, and thaw depth in mid-August 1999. Abbreviations as in Table 3

| Variable | Factor | | | | | | | | | | | |
|---------------------|--------|-------|----------|------------------------|-------|----------|--------------------|-------|-----------|---------|-------|----------|
| | Block | | | Neighbour removal (NR) | | | Fertilization (Ft) | | | NR × Ft | | |
| | Nd.f. | Dd.f. | F | Nd.f. | Dd.f. | F | Nd.f. | Dd.f. | F | Nd.f. | Dd.f. | F |
| NH ₄ -N§ | 5 | 62 | 0.814 NS | 7 | 62 | 6.402*** | 1 | 62 | 92.577*** | 7 | 62 | 3.037** |
| NO ₃ -N§ | 5 | 62 | 0.582 NS | 7 | 62 | 5.931*** | 1 | 62 | 33.512*** | 7 | 62 | 0.984 NS |
| PO ₄ -P‡ | 5 | 56 | 0.632 NS | 7 | 56 | 2.244* | 1 | 56 | 130.68*** | 7 | 56 | 0.369 NS |
| Soil temperature | 5 | 75 | 0.420 NS | 7 | 75 | 0.875 NS | 1 | 75 | 2.827† | 7 | 75 | 0.579 NS |
| Thaw depth | 5 | 75 | 0.690 NS | 7 | 75 | 0.333 NS | 1 | 75 | 0.071 NS | 7 | 75 | 1.597 NS |

§Data were ln-transformed to achieve homogeneity of variance.

‡Data were rank-transformed, because homogeneous data could not be obtained by other transformations. Qualitative results of the non-parametric ANOVA on ranks were the same as obtained by parametric ANOVA.

positive, while non-vascular plants responded negatively or not at all. Graminoids responded most strongly to fertilizer addition, which is consistent with short-term results of previous fertilization experiments in tundra (Chapin *et al.* 1995; Chapin & Shaver 1996; Graglia *et al.* 2001; Shaver *et al.* 2001).

Most plant species did not respond to neighbour removal after 2 years of treatment, although some removal treatments caused an increase in graminoid biomass under fertilization, probably in response to increased nutrient availability. Also, the dominant forb, *Pedicularis* spp., decreased in all treatments that involved removal of *Ledum palustre*, indicating possible facilitation. Most species of *Pedicularis* are root hemiparasites with relatively non-specific host preferences (Nilsson & Svensson 1997; Sprague 1962), but our *Pedicularis* may have used *L. palustre* as their predominant host species in the plots.

Inorganic soil nutrient availability in 1999, however, increased greatly under both removal and fertilization. Nutrient availability was not measured in most previously published removal experiments (Jonasson 1992; Shevtsova *et al.* 1995; Shevtsova *et al.* 1997; Hobbie *et al.* 1999), although removal of all vascular plants has been reported to increase NH₄⁺ availability in soil solution over the winter (Grogan & Jonasson 2003). In our experiment, removal of either mosses or large amounts of vascular plant biomass increased soil nutrient availability to a greater extent than fertilization in the intact community.

Productivity in tussock tundra is nutrient-limited (Shaver & Chapin 1980; Chapin & Shaver 1985; Shaver & Chapin 1986; Chapin *et al.* 1995; Shaver *et al.* 2001), and our experiment showed responses to fertilizer addition. Greater responses of plant biomass to neighbour removal might therefore be expected. Tundra plants might, however, have such rigidly defined, and complementary, niches for nitrogen uptake that they cannot take up nutrients made available by neighbour removal. Different natural abundance ¹⁵N signatures among tundra plant species (Nadelhoffer *et al.* 1996), and differences in the timing, depth and uptake of different chemical forms of nitrogen suggest that niche differentiation for N uptake provides a basis for the coexistence of plant

species in tussock tundra (McKane *et al.* 2002). Rigid niche differentiation is consistent with results of previous removal experiments in (unfertilized) arctic tundra, which showed few significant effects on biomass of remaining plants (Jonasson 1992; Shevtsova *et al.* 1995; Shevtsova *et al.* 1997; Hobbie *et al.* 1999). These results are also consistent with the suggestion (Grime 1977, 1979) that competition is less important in structuring communities under stressful environments, including conditions of low nutrient availability, such as are seen in the Arctic. However, positive interactions might be more common and important in arctic or alpine environments than in milder climates, because neighbours could ameliorate harsh physical conditions (Callaghan & Emanuelsson 1985; Bertness & Callaway 1994; Brooker & Callaghan 1998). In contrast to arctic tundra, removal experiments in alpine tundra have shown both positive and negative species interactions (del Moral 1983; Theodose & Bowman 1997; Aksenova & Onipchenko 1998; Gerdol *et al.* 2000; Choler *et al.* 2001), and facilitation is more common under stressful conditions (Callaway *et al.* 2002).

Alternatively, insufficient time may have elapsed, after nutrients were released by neighbour removal, for tundra plants to take them up, alter their growth and show a change in biomass. Most arctic and alpine plants preform buds over one or more prior growing seasons (Aydelotte & Diggle 1997; Diggle 1997), and many have deterministic shoots, and may therefore only be able to increase their growth in response to increased nutrient supply after several seasons. In previous fertilization experiments in tussock tundra, there was a lag of 2–3 years before *Betula nana* increased its branching rate, after which it showed rapid and sustained growth (Bret-Harte *et al.* 2002). Nutrients made available by neighbour removal, as observed in 1999, are likely to have been present for a shorter period of time than those added as fertilizer, because regrowth in 1997 and 1998 from surviving underground portions of the removed species would have continued to absorb nutrients. If this explanation is correct, effects of removal treatments on growth may not become evident until after a longer time lag.

Several mechanisms could contribute to increased nutrient availability in the removal treatments. First, removal reduced the total plant uptake of nutrients, because community biomass had not returned to pre-treatment levels by 1999, and soil microbes may not have been able to completely absorb the excess. The additional nutrients available to plants from fertilizer probably comprised less than 20% of that applied, at least initially, because of physical and microbially mediated immobilization (Marion *et al.* 1982); this is at most about three times the estimated annual plant N uptake in control tundra (Shaver & Chapin 1991). Most vascular plants increased biomass under fertilization, presumably as a result of nutrient uptake, but nutrient availability in fertilized removal treatments was much greater than in the fertilized intact community. This must have resulted in part from decreased total nutrient uptake by the plant community because of smaller amounts of vascular plant biomass.

It is likely that plants took up some nutrients made available by neighbour removal, as well as those from applied fertilizer. Tundra plants normally meet 75% of their annual N requirement from stored reserves (Shaver & Chapin 1991), which implies that plants can divert new uptake of nutrients into storage if growth capacity is not immediately available. Neighbour removal increased NH_4^+ availability less than either NO_3^- or PO_4^- in unfertilized plots. NH_4^+ is more abundant than NO_3^- in control tundra (Giblin *et al.* 1991), and is readily taken up by tundra plant roots in solution culture (Kielland 1994), although some tundra plants also take up NO_3^- (McKane *et al.* 2002). NH_4^+ made available by species removal may have been taken up more readily by plants or microbes than NO_3^- . Changes in composition and abundance of *Betula* mycorrhizas in *Ledum* removal plots were similar to those seen under fertilization (Urcelay *et al.* 2003), suggesting that *Ledum* removal made nutrients available to *Betula*, even though they did not accumulate on resins in that treatment.

Another mechanism that could contribute to increased soil nutrient availability is that microbial mineralization of N and P may have increased following neighbour removal. Nutrient mineralization from decomposition of dead roots might be expected to be higher in removal plots. However, high quality root carbon should promote microbial immobilization of nutrients (though perhaps not as much as above-ground litter containing less nitrogen) (Hobbie 1996; Hobbie *et al.* 2002). Removal of all vascular plants using methods very similar to ours did not change the dynamics of microbial C and N processing and retention in a subarctic birch forest, even though soil N availability increased (Grogan & Jonasson 2003), suggesting that this mechanism is relatively unimportant in vascular plant removal treatments.

Altered microbial processing of N and P may be a more major factor following moss removal. We initially expected that removal of the dense, insulating moss cover would increase soil temperature and depth of thaw, and that higher soil temperature might eventually

stimulate decomposition and lead to higher soil nutrient availability (Van Cleve *et al.* 1991; Hobbie 1995; Chapin *et al.* 1996). Increased nutrient availability in plots from which moss was removed cannot, however, be explained by changes in soil temperature and depth of thaw, which did not vary. Mosses do not have roots and therefore do not take up nutrients from the same soil pools as vascular plants do. Nutrient availability may have increased under moss removal because remaining dead moss bases are such a poor source of labile carbon that microbial mineralization, rather than immobilization, was induced (Hobbie 1996; Jonasson & Shaver 1999). Altered physical conditions at the soil surface might further have enhanced mineralization. Both mechanisms, increased microbial mineralization and reduced total plant uptake, are likely to have contributed to the increased nutrient availability observed in neighbour removal treatments.

Although our short-term results suggest that plant competition is not important, increased proportions of long shoots on *B. nana* under both moss removal and fertilization suggest that species interactions may become more important over the longer term. Long-term fertilization experiments in tundra show dramatic changes in the relative dominance of different species, suggesting that competition for light, at least, is important under increased nutrient availability (Bret-Harte *et al.* 2001; Shaver *et al.* 2001). Shifts in the proportion of long shoots in *B. nana* preceded a massive growth response in previous fertilization experiments (Bret-Harte *et al.* 2001; Bret-Harte *et al.* 2002), and *Sphagnum* removal significantly increased *B. nana* biomass after three and a half years (Hobbie *et al.* 1999). In temperate ecosystems, Gurevitch & Unnasch (1989) observed different effects of removal of a dominant species at high and low soil fertility, and fertilization often leads to dominance of one or a few species (Silvertown 1980; Huenneke *et al.* 1990).

Increased availability of inorganic nutrients in unfertilized species removal plots suggests that appreciable N could be lost from living components of the ecosystem, either through leaching or denitrification, if the remaining plants cannot adjust to retain more of this N. Inorganic nutrient availability is normally low in tundra, and more than 99% of the N is sequestered in undecomposed organic matter (Chapin *et al.* 1980). Most of the N added to tussock tundra over 20 years of fertilization has not been retained, even though some plant species have benefited greatly (M. Mack, unpublished data). Tundra might be particularly vulnerable to loss of nutrients under a changing climate, because the strong environmental filter imposed by the arctic climate has created a regional plant species pool that contains almost no ruderal species capable of quickly taking advantage of increased nutrient availability. Conversely, if climate warms enough to allow weedy species to persist in the Arctic, changes in species composition that result in higher levels of available nutrients may allow rapid invasion and establishment of exotic plant species.

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References

- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.
- Aksenova, A.A. & Onipchenko, V.G. (1998) Plant interactions in alpine tundra: 13 years of experimental removal of dominant species. *Ecoscience*, **5**, 258–270.
- Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Aydelotte, A.R. & Diggle, P.K. (1997) Analysis of developmental preformation in the alpine herb *Caltha leptosepala* (Ranunculaceae). *American Journal of Botany*, **84**, 1646–1657.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Bliss, L.C. & Matveyeva, N.V. (1992) Circumpolar arctic vegetation. *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective* (eds F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda), pp. 59–89. Academic Press, San Diego.
- Bret-Harte, M.S., Shaver, G.R. & Chapin, F.S. III (2002) Primary and secondary growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology*, **90**, 251–267.
- Bret-Harte, M.S., Shaver, G.R., Zoerner, J.P., Johnstone, J.F., Wagner, J.L., Chavez, A.S. *et al.* (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology*, **82**, 18–32.
- Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos*, **81**, 196–207.
- Callaghan, T.V. & Emanuelsson, U. (1985) Population structure and processes of tundra plants and vegetation. *The Population Structure of Vegetation* (ed. J. White), pp. 339–439. Junk, Dordrecht.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R.J. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Chapin, F.S. III (1983) Direct and indirect effects of temperature on arctic plants. *Polar Biology*, **2**, 47–52.
- Chapin, F.S. III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. (1996) Plant functional types as predictors of the transient response of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347–358.
- Chapin, F.S. III, Miller, P.C., Billings, W.D. & Coyne, P.I. (1980) Carbon and nutrient budgets and their control in coastal tundra. *An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska* (eds J. Brown, P.C. Miller, L.L. Tieszen & F.L. Bunnell), pp. 458–482. Dowden, Hutchinson & Ross, Stroudsburg.
- Chapin, F.S. III & Shaver, G.R. (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564–576.
- Chapin, F.S. III & Shaver, G.R. (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology*, **77**, 822–840.
- Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Response of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- Choler, P., Michalet, R. & Callaway, R. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.
- Diaz, S., Symstad, A.J., Chapin, F.S. III, Wardle, D.A. & Huenneke, L.F. (2003) Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution*, **18**, 140–146.
- Diggle, P.K. (1997) Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. *American Journal of Botany*, **84**, 154–169.
- Flanagan, P.W. & Van Cleve, K. (1983) Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Canadian Journal of Forest Research*, **13**, 795–817.
- Gerdol, R., Brancaloni, L., Menghini, M. & Marchesini, R. (2000) Response of dwarf shrubs to neighbour removal and nutrient addition and their influence on community structure in a subalpine heath. *Journal of Ecology*, **88**, 256–466.
- Giblin, A.E., Nadelhoffer, K.J., Shaver, G.R., Laundre, J.A. & McKerrow, A.J. (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecological Monographs*, **61**, 415–435.
- Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*, **89**, 428–439.
- Gough, L., Wookey, P.A. & Shaver, G.R. (2002) Dry heath arctic tundra response to long-term nutrient and light manipulations. *Arctic, Antarctic, and Alpine Research*, **34**, 211–218.
- Graglia, E., Jonasson, S., Michelsen, A., Schmidt, I., Havström, M. & Gustavsson, L. (2001) Effects of environmental perturbations on abundance of subarctic plants after three, seven, and ten years of treatments. *Ecography*, **24**, 5–12.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester.
- Grogan, P. & Jonasson, S. (2003) Controls on annual nitrogen cycling in the understory of a subarctic birch forest. *Ecology*, **84**, 202–218.
- Gurevitch, J. & Unnasch, R.S. (1989) Experimental removal of a dominant species at two levels of soil fertility. *Canadian Journal of Botany*, **67**, 3470–3477.
- Harte, J., Torn, M.S., Chang, F.-R., Feifarek, B., Kinzig, A.P., Shaw, R. *et al.* (1995) Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications*, **5**, 132–150.
- Hobbie, S.E. (1995) Direct and indirect species effects on biogeochemical processes in arctic ecosystems. *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences* (eds F.S. Chapin III & C. Körner), pp. 213–224. Springer-Verlag, Berlin.
- Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503–522.

- Hobbie, S.E., Miley, T.A. & Weiss, M.S. (2002) Carbon and nitrogen cycling in soils from acidic and nonacidic tundra with different glacial histories in northern Alaska. *Ecosystems*, **5**, 761–774.
- Hobbie, S.E., Shevtsova, A. & Chapin, F.S. III (1999) Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, **84**, 417–434.
- Holland, E.A., Dentener, F.J., Braswell, B.H. & Sulzman, J.M. (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry*, **46**, 7–43.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, **71**, 478–491.
- Hultén, E. (1968) *Flora of Alaska and Neighbouring Territories*. Stanford University Press, Stanford.
- Jonasson, S. (1988) Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **52**, 101–106.
- Jonasson, S. (1992) Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos*, **63**, 420–429.
- Jonasson, S. & Shaver, G.R. (1999) Within-stand nutrient cycling in arctic and boreal wetlands. *Ecology*, **80**, 2139–2150.
- Kaiser, J. (2001) The other global pollutant: nitrogen proves tough to curb. *Science*, **294**, 1268–1269.
- Kielland, K. (1994) Amino acid absorption by arctic plants: implications for plant nutrition and nutrient cycling. *Ecology*, **75**, 2373–2383.
- Marion, G.M., Miller, P.C., Kummerow, J. & Oechel, W.C. (1982) Competition for nitrogen in a tussock tundra ecosystem. *Plant and Soil*, **66**, 317–327.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B. *et al.* (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, **415**, 68–71.
- del Moral, R. (1983) Competition as a control mechanism in subalpine meadows. *American Journal of Botany*, **70**, 232–245.
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. & Linkins, A.E. (1992) Microbial processes and plant nutrient availability in arctic soils. *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective* (eds F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda), pp. 281–300. Academic Press, San Diego.
- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L. & McKane, R. (1996) ¹⁵N natural abundances and N use by tundra plants. *Oecologia*, **107**, 386–394.
- Nilsson, C.H. & Svensson, B.M. (1997) Host affiliation in two arctic *Pedicularis* species (Scrophulariaceae). *Ecography*, **16**, 154–166.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Shaver, G.R., Bret-Harte, M.S., Jones, M.H., Johnstone, J., Gough, L., Laundre, J. *et al.* (2001) Species changes interact with fertilizer addition to control 15 years of change in tundra. *Ecology*, **82**, 3163–3181.
- Shaver, G.R. & Chapin, F.S. III (1980) Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology*, **61**, 662–675.
- Shaver, G.R. & Chapin, F.S. III (1986) Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. *Arctic and Alpine Research*, **18**, 261–268.
- Shaver, G.R. & Chapin, F.S. III (1991) Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, **61**, 1–31.
- Shevtsova, A., Haukioja, E. & Ojala, A. (1997) Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated environmental conditions and species removal. *Oikos*, **78**, 440–458.
- Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M. & Haukioja, E. (1995) Growth and reproduction of dwarf shrubs in a subarctic plant community: annual variation and above-ground interactions with neighbours. *Journal of Ecology*, **83**, 263–275.
- Silvertown, J. (1980) The dynamics of a grassland ecosystem: botanical equilibrium in the park grass experiment. *Journal of Applied Ecology*, **17**, 491–504.
- Sprague, E.F. (1962) Parasitism in *Pedicularis*. *Madroño*, **16**, 192–200.
- Theodose, T.A. & Bowman, W.D. (1997) Responses of plant abundance and species diversity to nutrient availability in two alpine tundra communities. *Ecology*, **78**, 1861–1872.
- Urcelay, C., Bret-Harte, M.S., Diaz, S. & Chapin, F.S. III (2003) Mycorrhizal colonization mediated by species interactions in arctic tundra. *Oecologia*, **137**, 399–404.
- Van Cleve, K., Chapin, F.S. III, Dyrness, C.T. & Viereck, L.A. (1991) Element cycling in taiga forest: state-factor control. *Bioscience*, **41**, 78–88.
- Whitledge, T.E., Mallow, S.C., Patton, C.J. & Wirick, C.D. (1981) *Automated nutrient analysis in seawater*. Technical Report, Ocean Science Division, Brookhaven National Laboratory, Upton, New York.
- Winer, B.J., Brown, D.R. & Michels, K.M. (1991) *Statistical principles in experimental design*, 3 edn., McGraw-Hill, New York.
- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W. *et al.* (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.
- Walker, B., Kinzig, A. & Langridge, J. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95–113.
- Zar, J.H. (1999) *Biostatistical Analysis*. Prentice Hall, New Jersey.

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