The effects of NPK fertilization for nine years on boreal forest vegetation in northwestern Canada

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Abstract. Plant productivity is limited by mineral nutrient availability in many boreal forest ecosystems. This study is an analysis of the growth responses of components of a boreal plant community (cryptogams, herbaceous and woody perennials, the dominant shrubs *Salix glauca* (grey willow) and *Betula glandulosa* (bog birch) and the dominant tree *Picea glauca* (white spruce), to the addition of an NPK fertilizer over a nine-year period. The study was carried out in a low-nutrient boreal forest ecosystem in the Yukon territory in northwestern Canada. The following predictions were tested: (1) that there would be an overall increase in abundance (measured either as cover, density, or dry mass) of all components of the vegetation, (2) that vegetation composition would change as more competitive species increased in abundance and (3) that initial community changes in response to fertilization would be transient. In general, all predictions were found to be true. Species composition changed rapidly in response to fertilizer. Graminoids (e.g. *Festuca altaica*) and some dicots (e.g. *Mertensia paniculata* and *Achillea millefolium*) increased in cover, while other dicots (e.g. *Anemone parviflora*), dwarf shrubs (e.g. *Arctostaphylos uva-ursi*), bryophytes and lichens declined. There was a significant increase in the growth rate of the two dominant shrubs and of *Picea*, but not in the cone crop or seed production by *Picea*. Surveys after 1 or 2 years showed responses by the vegetation but more stable patterns of response did not emerge until after 5 or 6 years. There were consistent and directional changes in the percent cover of some of the herbaceous species on control plots. Growth rates of *Salix* and *Betula* varied considerably from year to year, independently of treatment. Long-term studies are essential if we are to understand the role of nutrient limitation in this ecosystem.

Keywords: Cone crop; Growth rate; Plant productivity; Seed production; Transient dynamics.

Nomenclature: Anderson (1959); Hultén (1964, 1968, 1970).

Abbreviations: KBFEP = Kluane Boreal Forest Ecosystem Project.

Introduction

Boreal forests occupy 12 million km^2, or 8 % of the world's continental ecosystems and account for ca. 12 % of the world's biomass (Whittaker & Likens 1973). Consequently, an understanding of their responses to perturbation will become increasingly important. Plant productivity has consistently been shown to be limited by mineral nutrient availability in boreal forest ecosystems (Larsen 1980; Van Cleve & Alexander 1981; Bonan & Shugart 1989; Nams et al. 1993; Schulze et al. 1994). Most fertilization studies in boreal ecosystems have monitored the response of selected components of the vegetation and usually report relatively short-term responses. As it is a multi-layered forest ecosystem, the response by the various components to enhanced nutrient levels will be complex and may not be easily predictable. Nevertheless, it is important to attempt generalizations about the response of the different kinds of plants of which it is composed.

The studies described are part of the larger Kluane Boreal Forest Ecosystem Project (KBFEP) conducted near Kluane Lake in the southern Yukon territory in northwestern Canada. A major objective of the KBFEP was to analyze interactions between the various trophic levels in the boreal forest using a series of experimental perturbations. The approach taken was to perturb different trophic levels and monitor the consequences on the populations or biomass of species in other levels. One of the perturbations involved the application of fertilizer to assess the impact of nutrient addition on the vegetation and subsequently on higher trophic levels especially on the amount of food available to herbivores. The response by all the major components of the plant community was variously measured as percentage cover, dry mass, growth rates or cone crops, allowing comparisons

to be made between the various components. In this paper, we report the results of many independent studies investigating the short-term and long-term growth responses of different components of boreal forest vegetation to fertilizer. In subsequent papers the impact of fertilizer addition at higher trophic levels will be reported.

We assumed that because most of the boreal forest is nutrient-limited the addition of fertilizer would increase the overall biomass of the vegetation at all levels. The most immediate response we expected to detect in the herbaceous layer and the more delayed response in the trees. Many studies have shown that plants differ in their ability to respond to increased nutrient levels (reviewed in DiTommaso & Aarssen 1989). Therefore, it was also expected that vegetation composition would change as those species able to respond to added nutrients replace those that could not. Specifically, we expected that, within the ground layer, graminoids and deciduous herbs would be able to respond more rapidly and positively to fertilizer addition than the evergreen dwarf shrubs and cryptogams. Finally, we wished to determine if initial community changes to the application of fertilizer would be transient (*sensu* Tilman 1988) and that more permanent shifts in vegetation composition would not be evident until after, perhaps, three or four years.

Study area

The boreal forest of North America is a continuous vegetation belt stretching across the continent and spanning more than 10° latitude. The climate (detailed in Hare 1954; Elliott-Fisk 1988; Bonan & Shugart 1989) is humid microthermal with very cold winters of 7 - 9 months duration allowing persistent snow cover except for a brief, relatively cool summer growing season, from mid-May to mid-August.

The studies reported here were done near Kluane Lake in the southern Yukon (138° 22' W; 61° 02' N) which is situated in the Shakwak Trench, a broad 8 - 14 km wide glaciated trench, 900 - 1000 m above sea level, between the Kluane and Ruby Ranges. Precipitation is low, with a mean annual average of ca. 230 mm, mostly falling as rain during the summer months; the average snowfall is about 100 cm. The vegetation is dominated by *Picea glauca* (white spruce), with a shrub understory dominated by *Salix glauca* (grey willow) and dwarf birches – primarily *Betula glandulosa* with some *B. nana*. The most abundant species in the herb and dwarf shrub layers are *Lupinus arcticus, Festuca altaica, Mertensia paniculata, Anemone parviflora, Achillea millefolium* var. *borealis, Linnaea borealis, Arctostaphylos uva-ursi* and *A. rubra, Epilobium angustifolium* and *Solidago multiradiata*. The primary vertebrate herbivores are snow-

shoe hares (*Lepus americanus*), Arctic ground squirrels (*Spermophylus parryi*), red squirrel (*Tamiasciurus hudsonius*), boreal red-backed vole (*Clethrionomys rutilus*) and voles of the genus *Microtus*; hereafter we will mostly use generic names only. Snowshoe hares are the dominant herbivore and they undergo a regular 9-10 year cycle where densities fluctuate several hundred fold. The last peak in hare densities was in 1990, followed by a rapid decline in 1991 and 1992. Boutin et al. (1995) and Krebs et al. (1995) describe detailed population changes in the vertebrate community. The first major impacts of an outbreak of spruce bark beetle were observed in 1995, but this had little impact on the results reported here.

Methods

Study sites

The first study (first section below) was done at two sites in areas of moderately open to dense white spruce forest (45 - 60 % canopy cover, typically 160 - 220 stems/ha) with a well-developed herbaceous understory (> 90 % cover). The first of these was at Boutillier summit (km 1690.4, Alaska Highway) and the second about 3 km to the south closeby the Microwave tower. The remaining studies (following sections) were done using four of the large 1-km² treatment grids from the KBFEP, specifically the two control grids, called Control 1 and Control 2 and the two fertilized grids, called Fertilizer 1 and Fertilizer 2. The fertilizer grids are 1-km² blocks of forest which were fertilized, using an aircraft, at the beginning of the growing season. Petri plates were placed on the ground throughout the fertilized area to sample the applied fertilizer and to confirm a fairly even distribution of fertilizer granules throughout the area. Preliminary studies indicated that the sites were generally nitrogen-limited so a nitrogen fertilizer was added in the first year. However, there were concerns that potassium and phosphorus limitation may occur once we had eliminated nitrogen limitation. For logistic reasons annual application rates were not always consistent but the standard was 17.5g N/m², 5g P/m² and 2.5g K/m². Nitrogen was added as $NH_4 NO_3$, phosphorus as H_3PO_4 and potassium as K_2O (Table 1). This rate is within the range used in other long-term fertilization experiments (Van Cleve & Zasada 1976; Weetman & Fournier 1984; Tamm 1985, 1991; Kellner 1993).

The various methods described in this work, especially to measure abundance, are variable because the studies were mostly independent and often had objectives beyond only the vegetation *per se*.

Table 1. Rates of fertilizer application for the Fertilizer 1, and Fertilizer 2 grids. Nitrogen was added as $NH_4 NO_3$, phosphorus as H_3PO_4 and potassium as K_2O.

Year	Fertilizer (kg ha^{-1})
1987	250 kg N
1988	175 kg N, 50 kg P, 25 kg K
1989	half 1988 rate
1990	175 kg N, 50 kg P, 25 kg K
1991	half 1988 rate
1992	no application
1993	175 kg N, 50 kg P, 25 kg K
1994	250 kg N
1995	no application

Herbaceous and cryptogamic vegetation - percentage cover on small plots

Eight $5 \text{ m} \times 5 \text{ m}$ plots were chosen at each of two sites, four fertilized and four control (no treatment). Granular fertilizer was applied by hand each year from 1990 to 1995, just after snowmelt between late May and early June. It was applied using 1988 KBFEP rates. Each plot was subdivided into five equal areas of $5 \text{ m} \times 1 \text{ m}$ and the fertilizer applied to one area at a time. Nitrogen was added as $NH_4 NO_3$, phosphorus as H_3PO_4 and potassium as K_2O.

In mid-June and mid-August each year a survey of the percent cover of all plant species less than 1 m tall was made on each plot. At every 10-cm point along five 4-m long transects, i.e. 200 points per plot, we placed a sampling pin and noted all different species whose leaves were intercepted by the pin; these point data were converted to percent cover. All mosses were recorded in a single category (moss), as were lichens in the genus *Peltigera* (mostly *P. canina*).

Percent cover data for each species were analyzed using the MGLH module in SYSTAT (Wilkinson et al. 1992). Data were $\log (x + 1)$ transformed before analysis. Treatment effects for each species were assessed using a repeated measures analysis of covariance on data from all surveys between August 1990 - August 1995, with the initial amount of the species present (June 1990) used as the covariate.

Herbaceous vegetation - presence and biomass on 1-km^2 plots

This study was done on the Fertilizer 1 and Fertilizer 2 grids and on areas within 100 m of these grids, which were unfertilized. On each of these four areas 80 sampling sites, each $1 \text{ m} \times 5 \text{ m}$, were chosen, 40 each in areas of closed spruce and open spruce forest. Closed spruce forest has > 70% tree canopy cover (typically > 600 stems/ha); open spruce has 25 - 50 % canopy

cover (typically 120 - 180 stems/ha; M. Nams unpubl.). For this study we chose the five herbaceous species which were both relatively abundant locally (between 3 - 10 % cover) and which were known to be readily grazed by snowshoe hares or other herbivores - *Epilobium*, *Mertensia*, *Lupinus*, *Achillea* and *Solidago*. Sampling of these herbaceous species was done during July in 1993 (7yr after fertilizer was first applied), 1994 and 1995, when herb biomass was at a peak. The location of each of the 320 sampling sites was permanently marked. Because sampling damages a site, several locations were selected at each site and a different location chosen each year. Within each sampling site a rooted frequency (number of individuals rooted within the $1 \text{ m} \times 5 \text{ m}$ site) was determined. The dry mass of five flowering and five non-flowering adult individuals of each species were randomly selected within each site. These were clipped at ground level, air-dried for one week, and used to determine mean above-ground biomass for each species.

Data were analyzed in two stages, to determine whether the experimental treatments affected (1) the probability that a given species was present and (2) the average size of plants. In all cases, variation between treatment grids, years and forest types (open or closed forest) was controlled in our analyses. Dry mass data for flowering and non-flowering plants were available only for *Achillea* and *Mertensia*; for the other species only data from either flowering (*Epilobium*) or non-flowering (*Lupinus* and *Solidago*) plants were collected. All species were not always present in all sites.

All data were analyzed using modules CATMOD, GLM and NESTED (Anon. 1989) in SAS. For ANOVAs type III sums of squares was used. The effects of fertilizer and of being in open or closed forest were considered 'fixed effects'. In contrast, years and grids were assumed to represent a random sample of all possible years and grids, and were treated as 'random effects'. Probabilities were calculated by taking the ANOVA tables generated by SAS and using the degrees of freedom and error terms for F-test as specified in Zar (1984) for a factorial ANOVA with two fixed and two random effects. Probabilities from presence/absence analyses were the predicted values produced by the logistic regression (Trexler & Travis 1993). Average mass was analyzed using analysis of variance. Mean values of plant mass and the errors around these are least squares means and their standard errors (e.g. Searle et al. 1980). Distributions of both sets of data were skewed and natural log transformation was used to normalize the data in all analyses.

Shrub growth

Salix glauca and *Betula glandulosa* are the two dominant shrub species at Kluane. Shrub growth was measured at the end of each growing season in late September on Fertilizer 1, Fertilizer 2 and both Control grids, for nine years from 1987 to 1995. This was done by clipping approximately 200 unbrowsed terminal twigs of 5 mm diameter of each species and weighing the fraction of these twigs that represent current year extension growth. Twigs were collected in the autumn before hare browsing occurred. Growth rings and color changes in the bark are used to identify new growth. In addition, twigs leave circular scars around the branch at the end of each growing season. By starting at the tip of a twig and counting these scars, one can separate the terminal material (current year's growth) from the older part of the twig. A 5-mm diameter sample typically represents 4 - 6 years growth. An index of growth in year t, G_t was determined using the measurement:

$$G_t = \frac{\text{Biomass of growth from current growing season } -t}{\text{Total biomass in autumn year t of a twig of 5 mm } \varnothing} \quad (1)$$

The 5 mm diameter was chosen because snowshoe hares typically browse twigs only up to that size. Growth rates were not normally distributed and were log-transformed for *Salix* and square root-transformed for *Betula* before analysis.

Shrub biomass

Standing crop of the two dominant shrubs (*Salix* and *Betula*) was measured at the end of winter in early May, before the growing season began; no leaves were present. Each year, from 1987 to 1995, all individual shrubs were clipped to ground level on 30 - 50 plots, each of $0.2 \text{ m} \times 10 \text{ m}$, on each of the two fertilized and two control grids. All clipped material was divided into two size classes, < 5 mm diameter and > 5 mm diameter; terminal dead branches were discarded. Clippings were wet weighed for both species by size class. A 50-g sample of each species and size class from each grid was collected and dried at 60 - 80 °C for 7 days to calculate a conversion factor from wet to dry weight. Biomass was log-transformed to estimate means and confidence limits and the arithmetic mean estimated with the Finney correction (Krebs 1989, p. 447).

Growth of Picea glauca

Spruce trees may respond to fertilizer addition in a variety of ways. For example, they may increase the amount of seed produced, the frequency of seed production, growth rates of shoots and roots and increase tissue quality.

Tree growth rates were determined by measuring lateral growth of branches each year. Spruce twigs grow from the distal end, and each year of growth is marked by a growth ring that circles the stem. The twigs produced during the most recent year of growth may have lateral buds but these buds do not grow into branches until the next year.

Trees were sampled on both of the fertilizer grids and both of the control grids. Twenty-five stations were selected at random from those classified as open spruce habitat (25 % - 50 % canopy cover, 120 - 180 stems/ha; M. Nams , unpubl.). At each station, three spruce trees with DBH > 10 cm were randomly selected. We began by sampling three branches on each tree but discovered that optimal subsampling required only one branch per tree (Krebs 1989, p. 23). On each tree a single branch was randomly selected and the length of growth for each year was recorded to the nearest mm. Growth in branch length was measured each year from 1986 until 1992. For each individual tree, growth was calculated as a proportional value of branch extension length expressed relative to the 1986 growth extension. This approach using ratios eliminates branch-to-branch and tree-to-tree variability in growth and highlights yearly growth differences. The observed ratios were analyzed as in Krebs (1989, p. 205).

Seed production and cone crops of Picea glauca

Red squirrels harvest many cones before they open. Consequently, seed production by spruce was measured by counting female cones and by collecting seeds. Counting cones on the trees in August is a measure of cone production and counting seeds is a measure of the amount of seed that escapes squirrel predation over the winter.

The production of spruce cones was monitored in early August from 1986 until 1994 on the two control and two fertilizer grids by examining the top 3 m (virtually all female cones are produced in this portion of the tree) of 86 trees on each grid. A visual estimate was made of the percentage of the top 3 m that is covered by the current year's cones. Pictures were also taken of trees that had more than 100 cones and the number of cones counted from the photograph.

Seed was collected at 80 systematically arranged sampling points on Fertilizer 1 and Control 1 using a single 28 cm diameter bucket (616 cm^2) at each point; logistic limitation prevented the sampling of Fertilizer 2 and Control 2. Each bucket was covered with a wire mesh to prevent access to seed predators. The buckets were set up in late August each year and collected the following May. Because of extreme skewness in the seed counts, bootstrapping methods were used to estimate confidence intervals and means (Manly 1991).
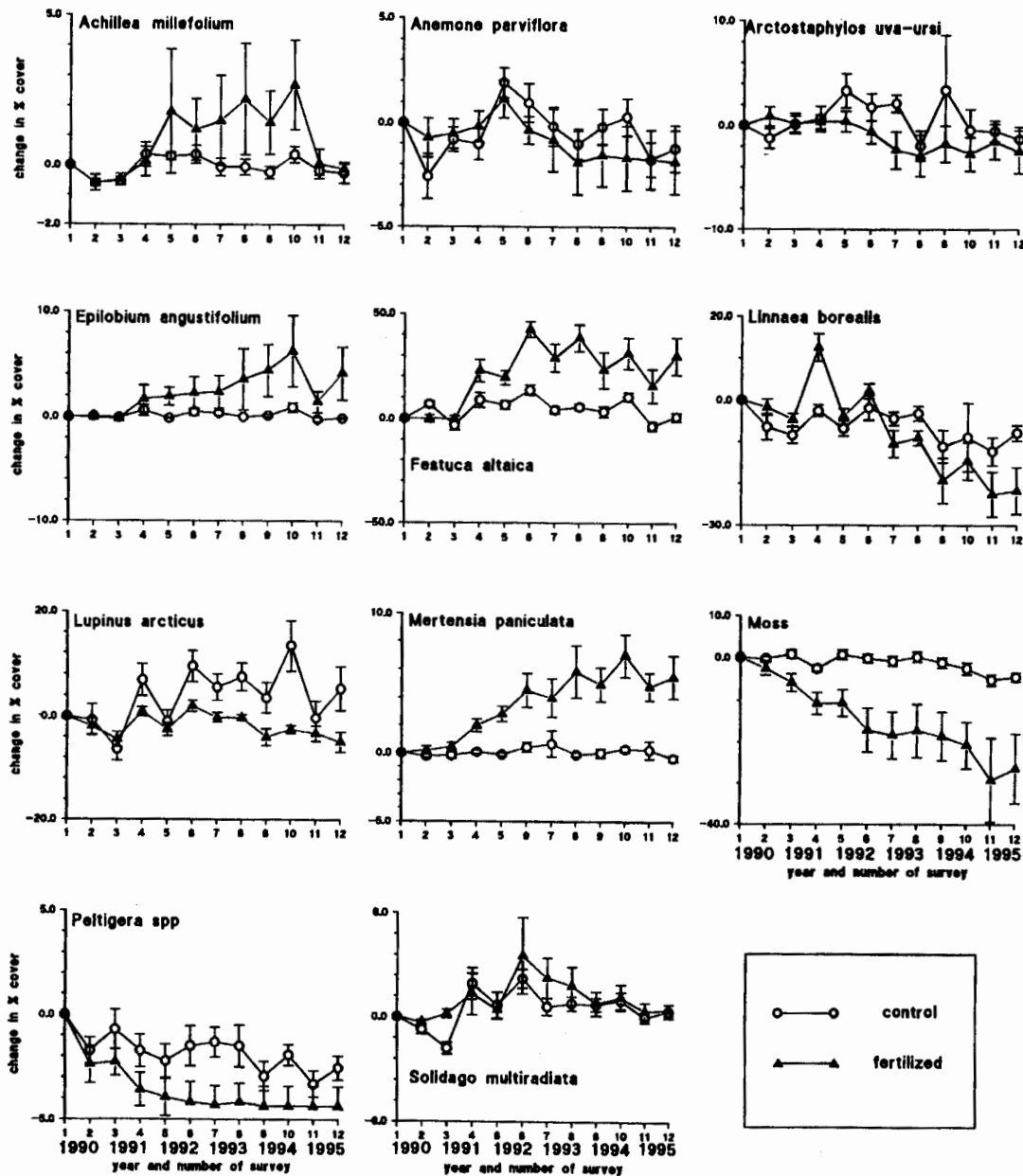
Fig. 1. Change in percent cover for species on fertilized (▲) and non-fertilized (O) plots at the Microwave and Boutillier Summit sites from 1990 to 1995. Fertilizer was first applied in May 1990, and is added each year in late May to early June. Odd survey numbers were taken in the spring and even numbers in the summer.

Results

Herbaceous and cryptogamic vegetation - percentage cover on small plots

Seven species showed significant percent cover responses to fertilizer after six years (Tables 2 and 7). Of these, three increased on the fertilized plots relative to controls (*Epilobium, Festuca* and *Mertensia*,

176 %, 173 % and 192 % respectively) and four declined (*Lupinus, Linnaea*, moss and *Peltigera*). Four species, *Achillea, Anemone, Arctostaphylos* and *Solidago*, did not respond significantly to the addition of fertilizer (Fig. 1) although some showed a consistent decline (*Anemone, Arctostaphylos*) after the first two years. *Achillea* and *Arctostaphylos* initially responded to fertilizer addition, but this effect was not consistent in all years. The negative response of *Linnaea* to fertilizer

Table 2. Probabilities from repeated measures Anova on the change in percent cover for species, in response to fertilization (F), in plots at the Microwave and Boutillier Summit sites (S) from 1990 to 1995 (Time). Significant values (p ≤ 0.05) are in bold. Symbols indicate whether effects are an increase (↑) or decrease (↓) in species abundance, or no change (=); some of the trends are not significant (ns).

	Achillea millefolium ↑(ns)	Anemone parviflora ↓ (ns)	Arctostaphylos uva-ursi ↓ (ns)	Epilobium angustifolium ↑	Festuca altaica ↑	Linnaea borealis ↓
Fertilizer (F)	0.252	0.074	0.214	**0.020**	**0.001**	**0.028**
Survey 1 (S)	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**
Time (T)	0.757	0.766	0.193	0.433	**0.000**	**0.032**
T × F	0.434	**0.000**	**0.001**	**0.003**	**0.000**	**0.000**
T × S	**0.022**	**0.000**	**0.017**	**0.000**	**0.000**	0.189

	Lupinus arcticus ↓	Mertensia paniculata ↑	Solidago multiradiata =	Peltigera spp. ↓	Mosses ↓
Fertilizer (F)	**0.004**	**0.000**	0.704	**0.000**	**0.012**
Survey 1 (S)	**0.000**	**0.011**	0.589	**0.020**	**0.000**
Time (T)	0.292	**0.000**	**0.000**	0.920	0.490
T × F	**0.008**	**0.000**	0.783	**0.000**	0.546
T × S	0.236	0.612	0.889	0.086	**0.000**

did not become apparent until later years. The community was relatively static on the control plots throughout the six years with most species showing remarkably little change. However, even on the control plots, some species such as *Lupinus*, *Anemone* and *Peltigera* naturally changed abundance.

Herbaceous vegetation - presence and biomass on 1 km² plots

The probability of *Mertensia* being present was greater on fertilized plots, regardless whether sites were open or closed forest (Fig. 2) and it produced more flowering stems in fertilized open sites (Fig. 3). Fertilization had a significant effect on *Achillea*, but only in open sites, and had little effect on *Solidago* in any sites.

The dry mass of non-flowering *Achillea*, *Epilobium* and *Mertensia* (Fig. 4) and flowering (Fig. 5), increased on closed sites when fertilized. The dry mass of *Achillea* and *Mertensia* increased in one of the fertilized sites (Fertilizer 1) but not in the other (Fig. 5). The dry mass of *Lupinus* consistently showed no response to fertilization (Fig. 5).

Overall we see a varied response by the herbaceous species to fertilizer with some increasing in abundance, others declining, and yet others remaining unchanged.

Shrub growth

Fertilization had a major effect on shrub growth especially from 1990-1995 (Table 3). Since 1987 *Salix* averaged 37 % higher growth indices on the fertilized

Table 3. Percent growth rates of terminal twigs of *Salix glauca* (grey willow) and *Betula glandulosa* (Bog birch) at Kluane Lake, Yukon. Twigs of 5 mm diameter are clipped and the growth rate is estimated as new growth/total twig weight for each twig. All data based on grams dry weight*. The sample size for each estimate is usually 200 twigs.

	1987	1988	1989	1990	1991	1992	1993	1994	1995
Salix glauca									
Control 1	12.3	13.0	12.1	13.7	14.3	10.6	9.6	8.0	8.5
Control 2	16.2	13.8	10.0	13.5	11.5	12.2	11.1	13.4	11.3
Fertilizer 1	11.3	11.7	12.2	17.0	21.6	15.7	12.2	11.5	13.7
Fertilizer 2	19.9	15.5	20.6	18.7	19.0	19.4	17.2	21.9	13.7
Betula glandulosa									
Control 1	8.9	10.6	24.6	-**	-	37.1	20.8	20.9	12.7
Control 2	7.2	12.1	9.5	6.7	-	-	-	-	-
Fertilizer 1	11.5	16.4	19.6	12.9	28.6	30.5	12.7	15.6	11.6
Fertilizer 2	12.2	15.7	17.2	22.9	27.2	30.5	18.5	21.2	17.7

* = Confidence limits are not given; all are ± 10 - 15 % of the estimate; ** = Severe browsing during the cyclic peak made it difficult to obtain samples of *Betula glandulosa* from control areas.
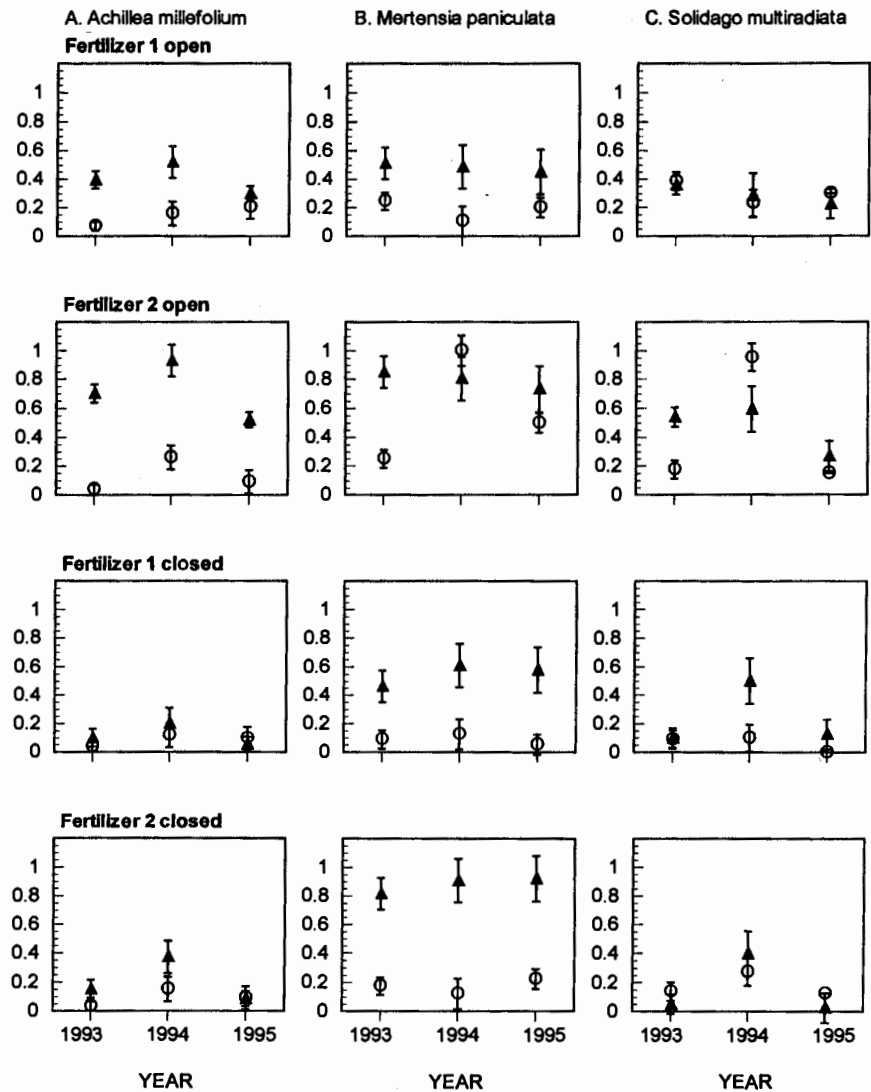
Fig. 2. Probability of **A.** *Achillea millefolium*, **B.** *Mertensia paniculata* and **C.** *Solidago multiradiata* being present on open and closed white spruce forest on fertilized (▲) and non-fertilized (O) plots. Error bars are 95 % confidence limits.

plots compared with the controls, while *Betula* averaged 146 % higher growth. Growth rates of shrubs varied considerably from year to year, independently of treatment (Table 3); the collapse of small twigs of both willow and birch in the control plots as hare densities increased to a peak in 1989-1990 (Boutin et al. 1995) is particularly dramatic (Figs. 6 and 7). Shrubs on fertilized plots were impacted less by increasing hare densities. *Betula* growth rates are particularly difficult to monitor just after the cyclic peak because it is difficult to find unbrowsed twigs.

Hare browsing increased until 1990, remained the same in 1991, and declined sharply in 1992-1993 (Table 4). During the peak years, more *Salix* twigs were browsed on the fertilized grids, but *Betula* twigs were impacted equally heavily on the control and fertilizer grids. In 1993-1995 browsing dropped to almost zero on all plots

because of low hare densities. *Betula* remained the favored species and only burial by snow prevented it from being completely eaten.

Shrub biomass

There were no clear trends in response of biomass to fertilization in the data for either *Salix* or *Betula*, and this is largely a reflection of the large variance among plots. The biomass of both small and large branches of *Betula* were always low relative to *Salix* from 1987 to 1994 (Table 5). The heavy browsing on *Betula* in 1990-91 resulted in a depression of small twig biomass for two years.
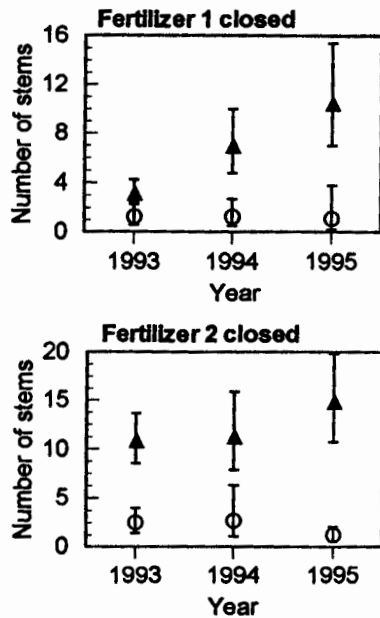
Fig. 3. Number of flowering *Mertensia paniculata* stems present per 5 m² on closed white spruce forest on fertilized (▲) and non-fertilized (O) plots. Expected values and their errors are from least squares means. Error bars are 95% confidence limits.

Growth of Picea glauca

Spruce trees had consistently more growth in fertilized sites compared to control sites in most years, although the differences were not always significant (Fig. 8). Trees responded by increasing twig growth by 15%-50% relative to pre-fertilization in 1986. Trees on both of the unfertilized control sites showed relatively consistent growth from 1987 to 1992, but differed through 1995. The magnitude of the response to the fertilizer treatment was unrelated to the amount of growth on the control plots (relative to 1986) (Fig. 8).

Seed production and cone crops of Picea glauca

Since 1986 there have been three years of almost complete *Picea* cone failure (1989, 1991 and 1994) (Fig. 9). In 1992, and particularly in 1993, cone production was well above other years and virtually all trees were heavily laden with cones. In 1988, 1993 and 1995, trees on the fertilized areas produced significantly fewer cones than those on control areas, but averaged over the entire nine-year period, there was no significant difference between fertilized and control sites.

Seed fall was also highly variable both spatially and temporally with generally low output from 1989 to 1992 (Table 6). There was a much greater output from 1993 to 1996. The highest seed output in both Control and Fertilized grids was in 1994 and this equates to 6.75 and 11.66 million seeds per hectare respectively; this was followed by a low interlude in 1995. We could detect no significant difference in seed production on the fertilized grid compared with the control area even though in six of seven years the fertilized area seemed to produce more seeds than the control areas.

Discussion

Although most boreal plant communities are nutrient limited, it is difficult to predict plant responses to environmental change especially in already harsh environments. Fertilization may affect factors important to plants in addition to soil fertility. For example, the addition of nitrogen fertilizer to a low-nutrient community will stimulate rapid microbial activity which, in the short term, will compete strongly for the added nitrogen, or may differentially promote the growth of some species, leading to changing light and moisture conditions for their neighbours. Some species in the community may not respond to an enhanced nutrient

Table 4. Percentage of twigs of *Salix glauca* (grey willow) and *Betula glandulosa* (bog birch) completely browsed by snowshoe hares at the end of winter, Kluane Lake, Yukon. Terminal twigs of about 5mm diameter were checked for browsing each May. Sample size for each estimate is 200 twigs of each species. (1987 = winter 1986-1987 browsing).

Salix glauca	1987	1988	1989	1990	1991	1992	1993	1994	1995
Control 1	0.0	13.5	9.2	18.3	16.7	1.4	0.6	0.0	0.5
Control 2	0.0	0.4	4.3	14.5	8.3	3.1	0.4	0.0	0.6
Fertilizer 1	0.0	2.5	14.3	40.6	46.9	1.1	0.8	0.0	1.7
Fertilizer 2	0.0	4.5	9.9	18.5	19.6	0.6	0.0	0.5	0.7

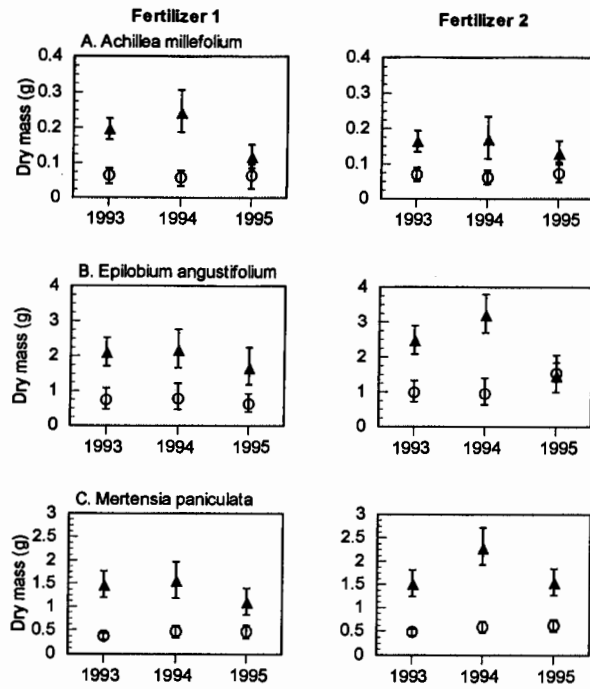| Betula glandulosa	1987	1988	1989	1990	1991	1992	1993	1994	1995
Control 1	0.0	6.0	76.7	66.7	71.0	3.6	0.0	0.0	0.0
Control 2	0.0	5.8	41.2	78.9	90.9	43.4	1.2	0.0	2.7
Fertilizer 1	0.0	4.5	41.1	73.8	67.2	0.0	0.0	0.0	0.0
Fertilizer 2	0.0	2.0	30.8	45.6	58.0	9.0	1.1	1.2	3.5

Fig. 4. Dry mass per plant of non-flowering **A.** *Achillea millefolium*; **B.** *Epilobium angustifolium* and **C.** *Mertensia paniculata* at two sites in closed white spruce forest. Each of the two sites (Fertilizer 1 and 2) had paired fertilized (▲) and non-fertilized (○) plots nearby. Expected values and their errors are from least squares means. Error bars are 95% confidence limits.
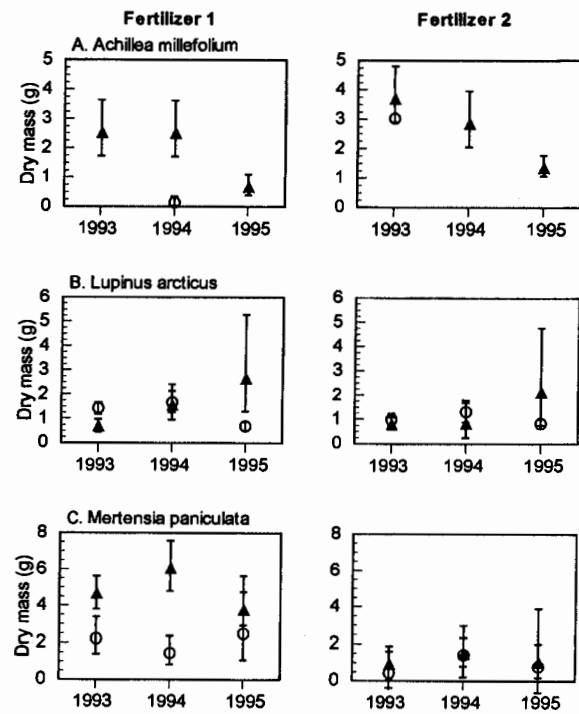
Fig. 5. Dry mass of flowering **A.** *Achillea millefolium*; **B.** *Lupinus arcticus* and **C.** *Mertensia paniculata* at two sites on closed white spruce forest on fertilized (▲) and non-fertilized (○) plots. Expected values and their errors are from least squares means. Error bars are 95 % confidence limits. *Achillea millefolium* was not found at all sites.

supply (Chapin et al. 1986). In this study, the abundance of some herbaceous species responded positively and others negatively or not at all to the addition of fertilizer, shrub growth rates increased but biomass did not, white spruce growth rate increased but cone crops and seed output did not (Table 7). *Festuca*, *Epilobium* and *Mertensia* showed the most obvious and immediate positive response to fertilization and this is consistent with that reported by Jonasson (1992). Because we applied fertilizer as an NPK mixture, it is not possible to separate their independent effects.

Table 5. Above-ground standing crop (grams dry weight per m²) of *Betula glandulosa* (bog birch) and *Salix glauca* (grey willow) at the end of winter, Kluane Lake, Yukon. Twigs of 5 mm diameter are separated from larger stems. Sample size for each grid is 30-50 quadrats of 2 m² each.

	Standing crop on May 1																	
	Betula glandulosa									*Salix glauca*								
	'87	'88	'89	'90	'91	'92	'93	'94	'95	'87	'88	'89	'90	'91	'92	'93	'94	'95
(A) Small branches (< 5 mm)																		
Control 1	0.2	0.0	0.1	0.1	0.0	0.2	0.1	0.2	0.1	31	11	23	33	26	30	17	21	23
Control 2	0.8	2.5	2.3	1.9	1.4	1.5	1.0	1.3	1.4	27	46	30	54	104	73	90	74	78
Fertilizer 1	8.6	2.4	2.0	5.7	3.0	3.3	7.1	9.1	7.0	39	20	47	24	27	53	38	61	31
Fertilizer 2	17.1	24.4	11.7	15.6	8.0	8.8	10.4	15.1	26.4	61	28	79	53	67	67	99	73	77
(B) Large branches (> 5 mm)																		
Control 1	0.0	0.0	0.0	0.1	0.0	0.4	0.1	0.3	0.1	47	17	73	139	115	163	58	113	122
Control 2	1.0	1.8	1.9	3.5	2.2	4.0	1.6	2.1	1.8	556	284	204	853	1704	1569	1034	1234	1046
Fertilizer 1	7.3	1.7	1.5	8.4	6.0	6.1	14.6	10.4	6.8	99	42	98	60	99	121	79	166	62
Fertilizer 2	39.5	63.8	26.1	53.6	36.0	44.5	44.2	66.5	50.3	816	317	1173	655	993	1086	1659	108.5	750.8

* Confidence limits not given in this table: all are large, about ± 40-50% of the estimate.

Table 6. White spruce seed counts on a control and a fertilizer area, 1989-1996. All data are per seed bucket. To convert to seed numbers per m², multiply these numbers by 16.31. Seeds counted in spring 1989 are from the seed fall of 1988-1989. Variability of seeds is not known. Confidence limits obtained by bootstrapping. c.l. = confidence limit.

Grid	Year of counts	Mean	Lower 95% c.l.	Upper 95% c.l.	Seeds/ ha (10⁶)	Sample size
Fertilizer #1	1989	2.4	1.7	3.4	0.39	83
	1990	0.0	0.0	0.0	0.0	40
	1991	4.5	1.5	13.6	0.73	81
	1992	0.2	0.0	0.3	0.03	40
	1993	10.6	6.1	80.0	1.73	81
	1994	71.5	39.7	145.5	11.66	69
	1995	0.6	0.0	2.6	0.1	39
	1996	44.2	10.1	116.6	7.21	83
Control #1	1989	1.9	1.0	4.2	0.31	82
	1990	0.0	0.0	0.0	0.0	40
	1991	2.1	0.3	9.2	0.34	85
	1992	0.1	0.0	0.1	0.02	39
	1993	7.9	4.1	13.7	1.29	85
	1994a	41.4	25.5	66.8	6.75	312
	1995	1.2	0.4	2.2	0.2	40
	1996	28.2	15.7	42.7	4.60	85

ªSamples lost. Mean of other unmanipulated areas.

Herbaceous vegetation

Studies of the effect of fertilization on the ground vegetation of boreal forests have produced somewhat conflicting results, partly because of the interaction with light limitation. In the study reported here, the effects of fertilizer addition on individual species within the herbaceous community range from no overall change to causing a dramatic increase or decline in abundance. There is clearly a range in the abilities of species to use the extra nutrients for increased growth (Chabot & Mooney 1985), and these differential changes in biomass will in turn affect inter-specific competitive relationships and lead to shifts in relative abundance and species diversity. *Epilobium*, *Festuca* and *Mertensia* increased dramatically in percent cover when fertilized, while *Anemone*, *Arctostaphylos*, *Linnaea* and other species decreased. Because *Festuca* is naturally much more abundant in the system than either *Epilobium* or *Mertensia*, visually it had the most obvious response to fertilization, even though the percentage increases were all quite similar. Two nitrogen fixing species (*Lupinus* and *Peltigera*) decline when fertilizer is added. It is likely that the declines following fertilizer addition in some species are due to them suffering increased competition from the more rapidly growing species. The results of this study are largely consistent with those of Nams et al. (1993) for the same species showing an increase in *Festuca*, *Achillea* and *Epilobium* following fertilization.

Understory changes are common after nitrogen application to boreal forests (Gerhardt & Kellner 1986; Dirkse & van Dobben 1989); lichens and bryophytes, typically decline (Kellner 1993; Mäkipää 1995), and grasses increase (Tamm 1991; Mäkipää 1995). Lichens and bryophytes have little or no protective cuticle and are likely to suffer from the direct effects of fertilizer toxicity, as some fertilizer granules land directly on their thallus or leaves. They also are low-growing and suffer the consequences of light limitation caused by the increased growth of taller neighbours in response to added fertilizer. Surprisingly, there were few differential responses by understory vegetation as a consequence of being in open or closed forest. Apparently the 'closed' forest with up to 70%
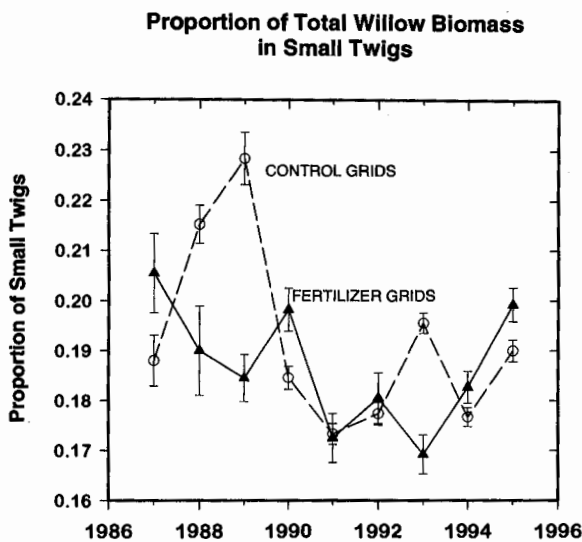
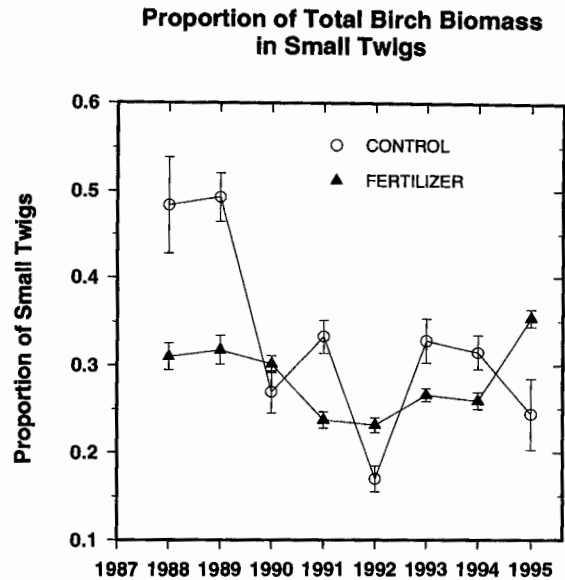**Fig. 6.** Proportion of total *Salix* biomass in small twigs.

Fig. 7. Proportion of total *Betula* biomass in small twigs

Table 7. A generalized summary of the growth responses to fertilization by some species in the boreal forest. For cryptogams, herbaceous species and dwarf shrubs, the magnitude of change in percent cover was calculated by comparing the relative change (between years 1990 and 1995) in fertilized and control plots; values for biomass are the changes from 1993 to 1995.

Species	Variable	Direction	Magnitude	Source
Cryptogams				
Lichens	percent cover	decrease	26%	Fig. 1
Moss	percent cover	decrease	25%	Fig. 1
Herbaceous species				
Achillea millefolium	percent cover	increase	22%	Fig. 1
	biomass	increase	33%	Fig. 4
Anemone parviflora	percent cover	decrease	124%	Fig. 1
Epilobium angustifolium	percent cover	increase	176%	Fig. 1
	biomass	increase	96%	Fig. 4
Festuca altaica	percent cover	increase	173%	Fig. 1
Lupinus arcticus	percent cover	decrease	119%	Fig. 1
	biomass	no change	-	Fig. 5
Mertensia paniculata	percent cover	increase	192%	Fig. 1
	biomass	increase	224%	Fig. 4,5
Solidago multiradiata	percent cover	increase	66%	Fig. 1
All species	percent cover	increase	18%	
Dwarf shrubs				
Arctostaphylos uva-ursi	percent cover	decrease	41%	Fig. 1
Linnaea borealis	percent cover	decrease	54%	Fig. 1
Shrubs				
Betula glandulosa	growth rate	increase	37%	Table 3
	biomass	no change	-	Table 5
Salix glauca	growth rate	increase	146%	Table 3
	biomass	no change	-	Table 5
Trees				
Picea glauca	twig growth	increase	15-50%	Fig. 8
	cone crop	no change	-	Fig. 9
	seed fall	no change	-	Table 6

canopy cover does not impose light limitation on the understory vegetation.

Chapin (1980) concluded that most plant species found in low productivity environments possess inherently low relative growth rates which may allow them to endure conditions of low nutrient availability. Such species often lack the flexibility to respond positively to increased resource availability. However, if some species in the community are able to respond to added fertilizer, then those that can not become vulnerable to local extinction when nutrients are increased. This may explain the negative response of *Linnaea* to fertilization; it is a low-growing dwarf shrub, which would be easily overtopped by taller neighbours with more plasticity in stature.

Shrubs

Some studies from the Arctic tundra have shown that the growth of evergreen dwarf shrubs is significantly stimulated by low levels of fertilization (Chapin & Shaver 1985; Henry et al. 1986) but higher levels of fertilization may lead to decline (Chapin & Shaver 1996) or mortality. Moderate fertilizer addition generally results in larger year-to-year fluctuations in productivity of individual species, but total community productivity remains relatively stable (Chapin & Shaver 1985). In most fertilization studies with solid fertilizers, dwarf shrubs decrease (Kellner & Mårshagen 1991). For example, Mäkipää (1994, 1995) reported that an increased nitrogen supply was deleterious to the dominant dwarf shrubs, mostly of the genera *Vaccinium* and *Calluna*. Our study demonstrated a large increase in
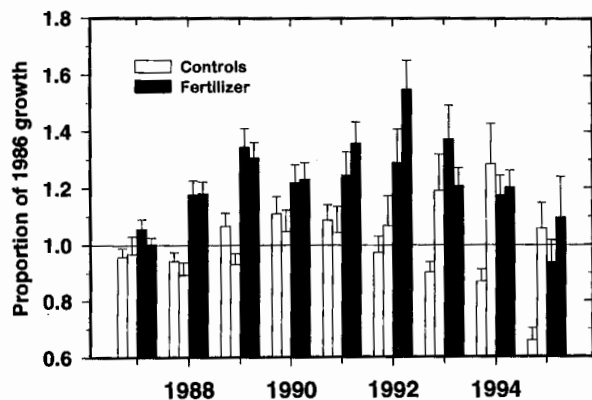

Fig. 8. Mean (± 1 S.E.) relative growth rates of distal branches of *Picea glauca* (white spruce) on two control grids and two fertilizer areas expressed relative to growth on the same branch in 1986 before fertilization.
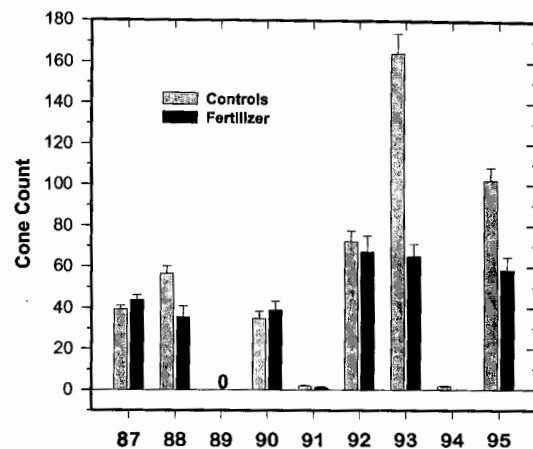

Fig. 9. Mean (± 1 S.E.) cone counts per individual *Picea glauca* tree in control and fertilized areas. There were no significant differences between counts on control and fertilized areas. Counts are taken from one position only and are an index rather than a total count.

growth rate by both *Betula* and *Salix*, but especially by *Betula*, to the addition of fertilizer for the duration of the study. *Betula* is favored by hares over *Salix* and only burial by snow prevents it from being completely eaten. Browsing was low in 1993, 1994 and 1995 on all areas because of low hare densities, and its positive response may not have been evident if browsing had been heavier.

It was predicted that fertilized plots would show an increased biomass relative to the unfertilized control plots and this should be particularly evident where we had demonstrated an increased growth rate. However, there are no clear trends in the standing crop data, and this is partly a reflection of two factors. First, snowshoe hares browse the twigs of both of the dominant shrubs and, especially during snowshoe hare peak densities, most of the new growth can be browsed. Therefore it is quite possible to get an increased growth rate without increased biomass. Second, there is very large variance among sample plots within our treatment areas.

Trees

In a 15-month study in our area, Nams et al. (1993) reported a 10% increase ($p < 0.01$) in growth rate of *Picea* (leader stem length) in response to fertilizer addition. In our study, spruce trees responded to fertilization in all years, increasing twig growth by 15 % - 50 % relative to pre-fertilization growth in 1986 (Fig. 8). Trees on both of the unfertilized control sites showed relatively consistent growth from 1987 to 1992, but differed through 1995. There is a large body of evidence to indicate that nitrogen availability is a primary limiting factor in most terrestrial habitats (Vitousek 1982) and for tree productivity in the boreal forest, so a positive growth response to added nitrogen is expected (Albrektson et al. 1977; Weetman & Fournier 1984; Tamm 1985, 1991). Van Cleve & Zasada (1976) thinned and fertilized a 70-yr-old white spruce stand in interior Alaska for five years (112 kg N/ha, 56 kg P/ha, 113 kg K/ha) using fertilizer levels that approximated those used in our study – lower N and higher K. Fertilization resulted in greater basal area increment than on the control site, but, in this case, differences were not always statistically different. Clearly, nutrient deficiencies are not the sole cause of growth limitation in these cold-dominated forest ecosystems. Alternatively, the trees may be absorbing the nutrients but transforming them into higher quality plant tissue (Mead & Tamm 1988) as well as into growth, or perhaps into defensive chemical compounds.

There was wide year-to-year variation in both the number of cones produced per tree and seed fall. There were three years of almost complete cone failure, yet in 1993 there was a high index of cone production. Nevertheless, trees on the fertilized areas did not produce a significantly different number of cones than those on control areas, but in those years when there was a cone crop, cones on fertilized trees produced more seed. This was most apparent in 1991 when seed counts on fertilized areas were double those on control areas and also in 1993, 1994 and 1996 when counts were increased by up to 80 % on fertilized grids. Seed counts can be heavily affected by red squirrel harvesting. Some of the apparent differences in seed production between the fertilized and control areas are possibly due to the artifact of the low red squirrel density on the fertilized grid (Boutin et al. 1995).

Long-term trends

It is apparent from this and other studies in this system (John & Turkington 1995, 1997) that populations of species on control plots vary within a season and between years. *Lupinus* percent cover increased on fertilized plots while *Linnaea* decreased. Likewise, growth rates of *Salix* and *Betula* varied considerably from year to year, independent of treatment. Whether this was determined in part by the dynamics of the snowshoe hare cycle (in which grazing is relaxed after the decline), yearly non-directional fluctuations in weather patterns (e.g. amount of rainfall), or some other trend (e.g. changing climate) may be determined by the continuation of this study through the next phase of the snowshoe hare cycle. The responses of both herbaceous species and shrubs varied from year-to-year and also within a growing season.

Transient dynamics and long-term studies

Within and between-year variation in populations and communities creates an important issue for experimental field ecology. In long-term experimental studies in the UK, (Grubb 1982), in Arctic tundra (Chapin et al. 1995; Chapin & Shaver 1996) and in Minnesota (Inouye & Tilman 1995) short-term vegetation responses, were poor indicators of longer term changes in community composition. Conclusions based on short-term responses to perturbations may simply reflect natural year-to-year variation, or transient dynamics (Tilman 1988) in the community. Therefore, the patterns and processes that seem most important in recently manipulated treatments may be of less importance in the undisturbed system. Tilman (1988) argues that transient dynamics should be a universal feature of terrestrial vegetation and that any experimental manipulation that increases resource availabilities should lead to a period of transient dominance where the initial responses will not mirror the long-term responses.

The results of our study emphasize this point. For

example, *Linnaea* initially responded positively to the addition of fertilizer and it wasn't until the fourth year of the study that its percent cover in fertilized plots started to decline. *Anemone* initially responded positively to nutrient addition, and it was only after several seasons that its decline became apparent. In part, this may have been due to the long-term nature of the changes being induced by the treatments, such as increased biomass of other species and the gradual accumulation of nutrients on fertilizer addition plots. A major concern also is the demonstration of a significant effect when one is not present; after nine years of fertilizer the standing crop biomass of neither *Betula* nor *Salix* showed a significant response. A survey done in 1990 would have shown a significant response by *Salix*, and a 1992 survey a significant response for *Betula*.

Long-term studies are particularly critical in systems where the species are long-lived and have limited rates of dispersal and establishment. For instance, at Cedar Creek, in communities dominated by herbaceous vegetation, changes in species composition were still occurring 10 years after the manipulations had taken place (Inouye & Tilman 1995). In systems such as the boreal forest understory it should be expected that new equilibrium conditions will be reached very slowly. But in contrast to the sandplain grassland communities at Cedar Creek, the boreal understory has limited physical disturbance of the vegetation and soil other than from grazing. Because of this, dispersal and establishment may be less critical processes than they are in more disturbed habitats.

Much of the information on fertilization effects on forest trees is derived from experiments where fertilizer applications have been made once or with intervals of several yeas. In such cases, many of the effects may also be transient. However, there are a few experiments in boreal forests where fertilizer additions have been repeated frequently over some years (but see Van Cleve & Zasada 1976; Weetman & Fournier 1984; Tamm 1985, 1991; Kellner 1993). Tamm (1991) concluded that the experimental treatments in the Swedish optimum nutrition experiments had created conditions that could be considered steady-state after about a decade. Weetman & Fournier (1984) reported a similar conclusion. In our study we fertilized regularly over a period of 8 years so it is likely that we were approaching stable responses by the trees. Fertilization of the herbaceous understory is continuing and results will be reported in a later paper.

In this paper we have documented various growth responses to added fertilizer of the different components of a boreal plant community. We have shown an overall increase in biomass of all components of the vegetation, with the most immediate response being detected in the herbaceous layer and the slowest response by the trees.

In addition, we have shown how vegetation composition changed as more competitive species replaced stress-tolerators. In future publications we will document more fully the detailed population dynamic responses of some of the individual species and the impact of fertilization at the higher trophic levels.

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