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 response of components of a boreal plant community (cryptogams, herbaceous and woody perennials, the dominant shrubs Salix glauca (gray 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 in 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 markedly in response to fertilization. Crinoids (e.g. Festuca altissima) and some dicots (e.g. Mentha arvensis and A. filifolia) increased in cover, while other dicots (e.g. Astragalus pumilus, 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.


Abbreviations: KBEFP = Kluane Boreal Forest Ecosystem Project.

Introduction

Boreal forests occupy 12 million km2, 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 (Larson 1980; Van Cleve & Alexander 1981; Thorn & Shugart 1989; Nams et al. 1993; Sublette 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 different kinds of plants of which it is composed.

The studies described are part of the larger Kluane Boreal Forest Ecosystem Project (KBEFP) conducted near Kluane Lake in the southern Yukon territory in northwestern Canada. A major objective of the KBEFP 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 in percentage cover, dry mass, growth rates or cone crops, allowing comparisons.
The bozoo forest of North America is a continuous vegetation belt stretching across the continent and spanning more than 10° latitude. The climax (detailed in Harr 1954; Efto et al. 1965; Bonal et al. 1985) is found in the interior west with very cold winters of 7-8 months duration allowing persistent snow cover except for a brief, relatively cold summer growing season from mid-May to mid-August.

The studies reported here were conducted near Klamath Lake in the southern Yukon (138° 27' WS; 6° 02' N) which is situated in the Shoshone-Trench, a broad 8-15 km wide glaciated trench, 500-1000 m above sea level, between the Klamath and Rocky 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 pine), with a shoot understory dominated by Salix glauca (tawny willow) and shrub birches — primarily Betula pumila. The shrub and herb layers are Littosius virgutus, Festuca alpina, Menziesia paniculata, Anemone pteris, Arctostaphylos uva-ursi, and Salix lasiolepis. The primary herbivores are snow

hoe hares (Lepus americanus), Arctic ground squirrels (Urocitellus parryi), two species (Drepanosomma hudsoni), beaver, red-backed voles (Clethrionomys rutilus) and voles of the genus Microtus, hereafter we will mostly use generic names only. Snowshoe hares are the dominant herbivores 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. Beaufort et al. (1995) and Korba et al. (1996) describe the detailed population changes in the vertebrate community. The first major impact of an outbreak of spruce bark beetles were observed in 1991, 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 an area of moderately open to intense white space forest (45° 06' N; 120° 20' W), typical of 220 m elevation with well-developed herbaceous understory (ca. 90% cover). The first of these was at Bozoo summit (km 690, Alaska Highway) and the second about 3 km to the south-densely forested Macroweaver site. The remaining studies (following sections) were done using four of the large 1 km² treatment grids from the KBEP, specifically the control grid, called Control 1 and 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. Five planes were placed on the ground throughout the fertilized area to simple the applied fertilizers and confirm a fairly even distribution of fertilizer granules throughout the area. Preliminary studies indicated that the sites were generally nitrogen limited so an analog fertilizer was added in the first year. However, these were concerns that potassium and phosphorus limitations may occur once we have eliminated nitrogen limitation. For logistic reasons annual application rates were not always consistent but the standard was 15 g N m², 3 kg P m² and 2.5 kg K m². Nisonger was added as NH₄NO₃, K₂CO₃ and as Ca₃(PO₄)₂ and potassium as K₂O (Table 1). This ratio is within the range used in other long-term fertilization experiments (van Cleve & Zasada 1973; Westman & Foresti 1984; Tamm 1985, 1991; Kjelvik 1993).

The various methods described in this work, especially for monitoring, abundance, are variable because the studies were mostly independent and often had objectives beyond only the vegetation per se.
Table 1. Rate of fertilizer application for the Fertilizer 1 and Fertilizer 2 grids. Nitrogen was added as NH₄NO₃, phosphorus as H₃PO₄ and potassium as K₂O.

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<th>Year</th>
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</tr>
<tr>
<td>1988</td>
<td>175 kg N, 50 kg P, 35 kg K half 1989 rate</td>
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<tr>
<td>1990</td>
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<tr>
<td>1991</td>
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<tr>
<td>1994</td>
<td>250 kg N, 50 kg P, 25 kg K</td>
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<td>1995</td>
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Herbaceous and cryptogamic vegetation - percentage cover on small plots

Eight 5 m x 5 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 KBEP rates. Each plot was subdivided into five equal areas of 5 m x 1 m and the fertilized applied to one area as a slit. Nitrogen was added as NH₄NO₃, phosphorus as H₃PO₄ and potassium as K₂O.

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 four 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 counts were converted to percent covers. All mosses were recorded in a single category (moos), as were lichens in the genus Peltigera (mainly P. cineraria). Percent cover data for each species were analyzed using the MGL 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-ha plots

This study was done on the Fertilizer 1 and Fertilizer 2 grids and on a series within 100 m of these grids, which were unfertilized. On each of these four areas 80 sampling sites, each 1 m x 5 m, were chosen. 40 each in areas of closed spruce and open spruce forest. Closed spruce forest has ≥70% tree canopy cover (typically >60 C stems/ha), open spruce has 25 - 50% canopy cover (typically 120 - 180 stems/ha, M. Namu unpublished). For this study we chose the five herbaceous species which were both relatively abundant locally (between 3 - 10% cover) and which were known as being grazed by snowshoe hare or other herbivores - Epipactis, Veratrum, 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 330 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 m x 5 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 Veratrum; for the other species only data from either flowering (Epipactis) 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 ANOVA 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 Zat (1994) 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. Steel et al. 1980). Disturbance 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 Khana. 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 unbudded terminal twigs of 5 mm diameter of each species and weighing the fraction of these twigs that represented current year extension growth. Twigs were collected in the autumn before leaf-browning occurred. Growth rings and cosine changes in the bark were used to identify new shoots. In addition, twigs leave circular scars around the branch at the end of each growing season. By marking at the tip of a twig and counting these scars, one can accurately determine 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, Gt was determined using the measurement:

\[ G_t = \frac{\text{Biases of growth from current growing season - 2}}{\text{True biomass in current year of a twig of 5 mm diameter}} \]  

(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 m × 10 m, or 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. Cappings were weighed for both species by size class. A 5-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 (Kees 1989, p. 447).

Growth of Picea glauca

Space 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 or shoot sizes and increase tissue quality. Tree growth rates were determined by growing 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 twig. 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 stenotopes). M. Nams., unsp.1. 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 (Kees 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 Kees (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 few 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 cone 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 150 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 cm²) 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 (Moody 1991).
Fig. 1. Change in percent cover for species on fertilized (A) and non-fertilized (C) plots at the Microwave and Coonkillie 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 Merenneria, 176 %, 173 % and 192 % respectively) and four declined (Lupinus, Linnaea, moss and Pelilgera). Four species, Achillea, Smilacina, Arctostaphylos and Solidago, did not respond significantly to the addition of fertilizer (Fig. 1) although some showed a consistent decline (Arctostaphylos, 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
did not become apparent until later years. The com-
unity 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, Astragalus, and Penstemon natu-
rally changed abundance.

**Herbaceous vegetation: presence and biomass on 1 ha plots**

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

| Salvia × arizonicum | *Antirrhinum* x 
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The dry mass of non-flowering *A. bifolium*, *Erythranth-
as*, and *Mertensia* (Fig. 4) increased with flowering (Fig. 5), increased
on closed sites when fertilized. The dry mass of *A. bifolium* 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 fertilize with some increasing in abundance, others declining, and yet others remaining unchanged.

**Skunk growth**

Fertilization had a major effect on skunk growth; especially from 1990-1995 (Fig. 3). Since 1997, salinity averaged 37% higher growth indices on the fertilized

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*Confidence intervals are not given; all are ± 10% of the estimate; **= severe burning during the cycle; male = difficulty in obtaining samples of intact plants from control areas.*
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 64 control plots at low densities increased to a peak in 1989-1990 (Boutin et al., 1995) is particularly dramatic (Figs. 6 and 7). Shrub on fertilized plots were impacted less by increasing hare density. 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 unfertilized 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 regained 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. 2. Probability of A. Achillea millefolium, B. Mertensia paniculata, and C. Solidago multiradiata being present on open and closed white spruce forest in fertilized (A) and non-fertilized (B) plots. Error bars are 95% confidence limits.
Seed production and cone crops of *Picea glauca*

Since 1980 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, 1991 and 1995, trees on the fertilized areas produced significantly fewer cones than those on control areas, but averaged over the entire six-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 1988 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 67 and 11.60 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 seeded to produce more seeds than the control areas.

**Discussion**

Although most beech mast compositions 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 neighbors. Some species in the community may not respond to an enhanced nutrient

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**Table 4. Percentage of twigs of Salix glauca (gray willow) and *Betula pumila* (birch) completely browsed by snowshoe hares at the end of winter, Khune Lake, Yukon.**

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**Fig. 3. Number of flowering *Menziesia pumilus* stems present per 5 m² on closed white spruce forest on fertilized (A) and non-fertilized (C) 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 the unfertilized control sites showed relatively consistent growth from 1987 to 1992, but differed through 1995. The magnitudes of the response to the fertilizer treatment was unrelated to the amount of growth on the control plots (relative to 1986) (Fig. 8).
Fig. 4. Dry mass per plant of non-flowering A. Achillea millofolium; B. Epilobium angustifolium and C. Mentha paniculata at two sites in closed white spruce forest. Each of the two sites (Fertilizer 1 and 2) had paired fertilized (A) and non-fertilized (B) plots nearby. Expected values and their errors were from least squares means. Error bars are 95% confidence limits.

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 Menthae 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 3 mm diameter are separated from larger stems. Sample size for each grid in 30-50 quadrats of 2 m² each.

<table>
<thead>
<tr>
<th>Standing crop on May 1</th>
<th>Betula glandulosa</th>
<th>Salix glauca</th>
</tr>
</thead>
<tbody>
<tr>
<td>97</td>
<td>98</td>
<td>99</td>
</tr>
<tr>
<td>Control 1</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Control 2</td>
<td>0.8</td>
<td>2.5</td>
</tr>
<tr>
<td>Fertilizer 1</td>
<td>8.6</td>
<td>2.4</td>
</tr>
<tr>
<td>Fertilizer 2</td>
<td>17.1</td>
<td>24.6</td>
</tr>
</tbody>
</table>

(A) Small branches (< 5 mm)

(B) Large branches (> 5 mm)

| Control 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Control 2 | 10.0 | 18.4 | 1.2 | 5.5 | 2.4 | 4.0 | 1.6 | 1.5 | 1.5 | 3.4 | 11.2 | 10.8 | 9.0 | 1.5 | 0.5 | 0.5 |
| Fertilizer 1 | 1.5 | 1.8 | 1.9 | 5.5 | 2.4 | 4.0 | 1.6 | 1.5 | 1.5 | 3.4 | 11.2 | 10.8 | 9.0 | 1.5 | 0.5 | 0.5 |
| Fertilizer 2 | 36.8 | 28.6 | 62.6 | 20.6 | 15.6 | 26.4 | 14.6 | 10.4 | 10.4 | 39.7 | 98.6 | 60.9 | 99.9 | 121.7 | 106.8 |

* Confidence limits are 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, 1986-1996. All data are per seed bucket. To convert to
seed numbers per m², multiply times numbers by 16.31. Seeds
counted in spring/summer are from the seed fall of 1988-1989.
Variability of seed is known. Confidence limits obtained by bootstrapping: cl = confidence limit.

<table>
<thead>
<tr>
<th>Grid</th>
<th>Year of counts</th>
<th>Mean</th>
<th>Lower 95% Cl.</th>
<th>Upper 95% Cl.</th>
<th>Mean/ha (100)</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertilizer</td>
<td>1989</td>
<td>2.4</td>
<td>0</td>
<td>2.4</td>
<td>0.39</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>1990</td>
<td>0.4</td>
<td>0.0</td>
<td>0.9</td>
<td>5.0</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>0.5</td>
<td>0.0</td>
<td>1.5</td>
<td>0.75</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.3</td>
<td>0.0</td>
<td>0.3</td>
<td>0.05</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>0.6</td>
<td>0.6</td>
<td>1.0</td>
<td>1.73</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>71.5</td>
<td>39.7</td>
<td>145.5</td>
<td>11.66</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>0.6</td>
<td>0.0</td>
<td>2.6</td>
<td>0.1</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>44.2</td>
<td>10.4</td>
<td>116.6</td>
<td>7.21</td>
<td>85</td>
</tr>
<tr>
<td>Control</td>
<td>1989</td>
<td>1.0</td>
<td>1.0</td>
<td>4.2</td>
<td>0.31</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>1990</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.05</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>0.1</td>
<td>0.0</td>
<td>0.2</td>
<td>0.34</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.0</td>
<td>0.0</td>
<td>0.1</td>
<td>0.02</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.02</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>4.4</td>
<td>25.8</td>
<td>68.8</td>
<td>6.75</td>
<td>512</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>1.2</td>
<td>1.5</td>
<td>2.2</td>
<td>1.74</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>28.2</td>
<td>18.7</td>
<td>42.7</td>
<td>4.00</td>
<td>83</td>
</tr>
</tbody>
</table>

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 herba-
cese community range from no overall change to a
dramatic increase in abundance. There is a
diversity in the abilities of species to use the extra
nutrients for increased growth (Chabot & Maxcy 1985),
and these differential changes in biomass will in turn affect
interspecific competitive relationships and lead to shifts in
relative abundance and species diversity. Epilobium, Festuca
and Menyanthes increased dramatically in percent
cover when fertilized, while Aruncus, Arctostaphylos,
Ligustrum and other species decreased. Because Festuca is
naturally much more abundant in the system than either
Epilobium or Menyanthes, visually it had the most obvious
response to fertilization, even though the percentage in-
creases were all quite similar. Two xerophytic species
(Euphorbia and Pelargonium) decline when fertilizer is added. It
is likely that the declines following fertilizer addition in
some species are due to them suffering increased competi-
tion from the more rapidly growing species. The results of
this study are largely consistent with those of Nurn et
al. (1993) for the same species showing an increase in Festuca,
Aruncus and Epilobium following fertilization.

Undesirable changes are common after almost any applica-
tion to boreal forests (Gehweiler & Kellner 1986; Dirks
def and van Dobben 1989; lichens and bryophytes, typically decline (Kellner 1993; Makiipii 1995), and grasses in-
crease (Tarri 1991; Makiipii 1995). Lichens and
bryophytes have little or no competitive outside and are likely
to suffer from the direct effects of fertilizer toxicity, as
some fertilizer granules land directly on their thalli or
leaves. They also are low-growing thus suffer the conse-
quencies of light limitation caused by the increased growth
of taller neighbours in response to added fertilizer. Surpris-
ingly, 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%
Table 7. A generalized summary of the growth responses to fertilization by some species in the boreal forest. For many species, biomass is the direct correlate of the positive response to fertilization, but for others, growth in diameter or height can also be important. The data presented are mean values from 1990 to 1995. The relative growth rates of these species are compared to the control plots in Fig. 6.

<table>
<thead>
<tr>
<th>Species</th>
<th>Variable</th>
<th>Direction</th>
<th>Magnitude</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crytocaryon</td>
<td>percent cover</td>
<td>increase</td>
<td>38%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>decrease</td>
<td>25%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>biomass</td>
<td>increase</td>
<td>22%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>biomass</td>
<td>decrease</td>
<td>33%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>12%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>decrease</td>
<td>16%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>95%</td>
<td>Fig. 4</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>119%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>192%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>226%</td>
<td>Fig. 4</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>46%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>18%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>43%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>decrease</td>
<td>54%</td>
<td>Fig. 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>37%</td>
<td>Table 3</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>146%</td>
<td>Table 1</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>51%</td>
<td>Table 3</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>35%</td>
<td>Table 2</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>decrease</td>
<td>5%</td>
<td>Fig. 6</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>25%</td>
<td>Fig. 6</td>
</tr>
<tr>
<td></td>
<td>percent cover</td>
<td>increase</td>
<td>15%</td>
<td>Fig. 6</td>
</tr>
</tbody>
</table>

Shrubs

Black spruce (Picea glauca) growth was significantly increased by fertilization. The relative growth of black spruce is shown in Fig. 6. The relative growth of white spruce (Picea glauca) was also significantly increased by fertilization. The data presented are mean values from 1990 to 1995. The relative growth rates of these species are compared to the control plots in Fig. 6.

White Spruce Cone Counts

Fig. 8. Mean (± 1 S.E.) relative growth rates of distal branches of Picea glauca (white spruce) on two control grids and two fertilizer grids, 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 grids on control and fertilized areas. Cones were taken from one position on each tree, and the index was taken from the 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 known to be fast-growing, but not faster than Salix. This study also showed that the addition of fertilizer increased growth rates of both species. However, there were no clear trends in the standing crop data, and this is partly a reflection of the fact that growth rates of both species varied significantly within each experimental area.

Trees

In a 15-month study in our area, Noms et al. (1993) reported a 10% increase in tree growth rate of Pinus (ponderosa pine) in response to fertilizer addition. To our study, spruce trees responded to fertilization in all areas. Increasing twig growth by 15%-50% relative to pre-fertilization growth in 1996 (Fig. 8). Trees on both of the unaltered control sites showed relatively consistent growth from 1997 to 1992, but differed significantly in 1995. There is a large body of evidence to indicate that nitrogen availability is a primary limiting factor in most terrestrial ecosystems (Yeow and Salix 1992) and for tree productivity in the boreal forest, so a positive growth response to added nitrogen is expected (Albrecktorsson et al. 1997, Woetman & Sjursen 1984, Yomota 1995, 1999). Van Cleve & Zedada (1976) determined fertilized 70-yr-old white spruce stand in interior Alaska for five years (12 kg/1ha, 35 kg/1ha, 113 kg/1ha) 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 translocating them into higher quality plant tissue (Meld & Yomota 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 high cone production, in 1992, 1993, and 1994, and a high index of cone production. Nevertheless, trees on the fertilized sites 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 1992 when seed counts on fertilized sites were significantly higher than on control areas and also in 1993, 1994, and 1995 when cones were increased by up to 80% on fertilized grids. Seed counts can be heavily affected by rain and snow harvesting. Some of the apparent differences in seed production between the fertilized and control areas are possibly due to the influence of the low red-squirrel density on the fertilized grid (Brown et al. 1995).

Long-term trends

It is apparent from this and other studies in this region (Brown & Turkington 1995, 1997) that populations of species on control plots vary without a seasonal or between-year. Lactating percent cover increased on fertilized grids while Lactation 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 related 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 confirmation of this study throughout the new 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

With this and between-year variation in populations and communities creates an important issue for experimental field ecology. In long-term experimental studies in the UK, (Grube 1982, in Arctic tundra (Chapin et al. 1995; Chapin & Sh Fake 1996) and in Minnesota (Insure & Tolson 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 to genetically manipulated environments 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 occludes resource availability should lead to a period of transient dominance when the initial responses will not reflect the long-term responses. The results of our study emphasize this point.
example, Litterer initially responded positively to the
addition of fertilizer and afterwardly to nitrate 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 particles
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 Breda nor Sult showed a significant
response. A survey done in 1996 would have shown a
significant response by Sult, and a 1992 survey a significant response for Breda.

Long-term studies are particularly critical in sys-
tems 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 (Thorns & Toms 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 stock-based 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 as 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 years. In such cases, many of the effects may also be transitory. However, there are few experiments in
boreal forests where fertilizer additions have been re-
peated frequently over some years; but see Van Cleve & 
Zanda 1976, Voetman, & Fournier 1984; Tanim 1985,
1991; Kelner 1993). Tanim (1991) concluded that the
experiment results in the Swedish optimum nutrition
experiment had created conditions that could be
considered steady-state after about a decade. Voetman &
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
controlling 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 tress.

In addition, we have shown how vegetation composi-
tion changed in response to fertilization and how this
response differed among forest sites. 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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