

Residual effects of NPK fertilization on shrub growth in a Yukon boreal forest

Michael C. Melnychuk and Charles J. Krebs

Abstract: Residual effects of nutrient additions were sustained in shrubs 4–8 years after fertilization stopped in a northern boreal forest in Yukon, Canada. We measured the growth rate of grey willow (*Salix glauca* L.) and bog birch (*Betula glandulosa* Michx.) twigs during the growing seasons of 1998, 2001, and 2002, 4–8 years after NPK fertilization from 1987 to 1994 had ceased. We also measured the nitrogen concentration of the 1998 growth tissue. Willow twigs had significantly higher growth rates in previously fertilized shrubs than control shrubs in these 3 years, even greater than differences observed during fertilization. Willow also had higher N concentration in fertilized twigs than control twigs. Birch growth was negatively correlated with hare abundance during the snowshoe hare (*Lepus americanus*) abundance cycle. Birch growth rate was higher in fertilized twigs than control twigs in 1998 during the hare peak, but fertilized birch twigs approached control levels by 2002 following the hare decline.

Key words: *Salix*, *Betula*, productivity, nitrogen, fertilizer, herbivory.

Résumé : Les effets résiduels d'applications de fertilisants se sont maintenus chez les arbustes, 4–8 ans après l'arrêt de la fertilisation, dans une forêt boréale nordique du Yukon, au Canada. Les auteurs ont mesuré le taux de croissance des rameaux de saules gris (*Salix glauca* L.) et de bouleaux glanduleux (*Betula glandulosa* Michx.), au cours des saisons de croissance de 1998, 2001, et 2002, soit 4–8 ans après que les fertilisations pratiquées de 1987 à 1994 eurent cessé. Ils ont également mesuré la teneur en azote dans les tissus formés en 1998. Les rameaux de saule montrent des taux de croissance significativement plus importants chez les arbustes préalablement fertilisés que chez les arbustes témoins, au cours de ces 3 années, des différences qui sont même plus importantes, que celles observées pendant la période de fertilisation. Le saule contient également de plus fortes teneurs en azote dans les rameaux fertilisés que dans les rameaux témoins. La croissance du bouleau montre une corrélation négative avec l'abondance du lièvre, au cours du cycle d'abondance du lièvre d'Amérique (*Lepus americana*). En 1998, chez les rameaux fertilisés, la croissance du bouleau est supérieure à celle des rameaux témoins, au cours du pic d'abondance du lièvre, mais les rameaux de bouleaux fertilisés se rapprochent des valeurs témoins, vers 2002, suite au déclin du lièvre.

Mots clés : *Salix*, *Betula*, productivité, azote, fertilisant, herbivorie.

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Introduction

Plant productivity in boreal forests is generally limited by mineral nutrient availability (Van Cleve and Alexander 1981). Increasing nutrient levels with the application of inorganic fertilizers has often resulted in short-term positive growth responses. Several studies have also reported long-term growth increases of trees in various forest types several years after fertilization stopped (e.g., Binkley and Reid 1985; Prescott et al. 1995; Weetman et al. 1995; Neilsen and Lynch 1998; Kishchuk et al. 2002), demonstrating that a pulsed disturbance of nutrient addition can produce long-term impacts on forest ecosystems. The lasting effects of added nutrients are less well known in other growth forms such as shrubs, despite these growth forms often being an

important component of nutrient cycling within forests. Further, these residual effects are poorly studied in northern boreal or subarctic ecosystems, where growth responses to added nutrients are likely to persist since growth rates are typically slow.

Eight years of NPK fertilization (1987–1994) near Kluane Lake in southwestern Yukon increased the growth rates of grey willow (*Salix glauca* L.) and bog birch (*Betula glandulosa* Michx.) (Turkington et al. 1998). It also increased the biomass of the dominant herbivore, the snowshoe hare (*Lepus americanus*), in 1990 during the peak of its 8–10 year abundance cycle (Sinclair et al. 2000). The main winter foods of snowshoe hares are twigs of willow and birch less than 5 mm diameter (Krebs et al. 2001). These two deciduous shrubs, which dominate the understory of the Kluane boreal forest, are thus an important compartment in the total nutrient flow within this ecosystem. Several studies have reported growth responses within a year of fertilization ending in *Salix* sp. and *Betula* sp. shrubs in Alaskan tundra (Shaver and Chapin 1980; Bret-Harte et al. 2001), northern Sweden (Weih and Karlsson 1999), and the Kluane region (Nams et al. 1992; Turkington et al. 1998), but longer-term residual effects after fertilization has ended have rarely been

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documented in shrubs despite their abundance in the understory of boreal forests around the world and their importance to herbivore communities. One exception is in arctic tussock tundra, where *Salix pulchra* and *Betula nana* stems showed positive growth responses 2 years after NPK fertilizer application ended, and total aboveground biomass of *B. nana* was higher 4 years after fertilization ended (Chapin and Shaver 1985).

In this study, we measured the residual effects of long-term NPK fertilization on the growth rate and tissue nitrogen concentration of grey willow and bog birch near Kluane Lake, Yukon. In the 1998, 2001, and 2002 growing seasons, we compared shrubs growing in plots where fertilization ended in 1994 with those growing in nearby unfertilized plots.

Materials and methods

The boreal forest at Kluane Lake (61°N, 138°W, 900–1000 m a.s.l.) is relatively dry with a yearly average of 230 mm of precipitation, 57% of which falls as rain during the summer months (Turkington et al. 1998). The vegetation in the study area is dominated by white spruce (*Picea glauca*), with shrubs especially abundant in open areas. The above-ground shrub biomass averaged over all sites is 98.1% grey willow and 1.25% bog birch; willow is dominant on all study plots and birch is much patchier in its distribution (Krebs et al. 2001). Fertilizer was aerially applied in granular form over two 1-km² plots in June of each year from 1987 to 1994, at the beginning of each growing season. An average of 150 kg·ha⁻¹ N (applied as NH₄NO₃), 25 kg·ha⁻¹ P, and 12.5 kg·ha⁻¹ K was applied annually (Turkington et al. 1998).

To measure growth rate, willow and birch twigs from individual shrubs were sampled over 35 ha on three control and three fertilized plots in autumn after the growing season between 1987 and 1995. Shrub growth data over this period from two control and two fertilized plots were transformed for normality and previously reported in Turkington et al. (1998). Following this study, willow and birch twigs were sampled on two of the control plots in autumn after the growing season between 1996 and 2002 as part of a monitoring program. We sampled willow twigs on two of the fertilized plots in autumn after the growing season in 1998, 2001, and 2002. Since bog birch distribution is patchy and unbrowsed twigs are rare during the peak abundance of snowshoe hares (Turkington et al. 1998), we found adequate birch samples on only one of the fertilized plots in 1998, but on two plots in 2002. Sampling units are individual twigs from shrubs spaced a minimum of 15 m apart. One unbrowsed twig per shrub was clipped at 5 mm diameter by moving from the distal part of the twig down until the first point where the twig reached 5 mm. Snowshoe hares typically browse twigs up to this size (Smith et al. 1988). Twigs were frozen over the winter, then dried at 60 °C for 4 d the following spring. The previous year's growth was separated from the rest of the 5-mm twig based on differences in bark colour, growth scars, presence of resin glands in bog birch, and presence of hairs in grey willow (Turkington et al. 1998; Krebs et al. 2001). A growth index was estimated as the percentage of current annual growth in the total dry weight of

the 5-mm twig (Turkington et al. 1998). This index was chosen to correct for different twig weights because 5-mm twigs differ greatly in biomass (the coefficient of variation for biomass of 5-mm twigs from 1987 to 1995 was 46% for birch and 33% for willow). We also present statistical analyses using an alternative measure of growth, biomass of current annual growth from 5-mm twigs, which give similar results to those using our growth index.

To present growth rates, means and bias-adjusted 95% confidence limits were bootstrapped from measured twig samples because growth rate distributions deviated from normal (Efron and Tibshirani 1986; Krebs 1999). We have plotted means of both the raw and bootstrapped data, and differences in growth rates between them were within 0.15% (i.e., their ratio was >0.96) in all years. We present the bootstrapped means, since they are more accurate when data are non-normal (Krebs 1999). Bootstrapped 95% confidence limits are preferable to standard errors of the mean because they provide an estimated range of values that is likely to include the unknown population mean, and the asymmetric confidence intervals produced are more appropriate for continuous distributions limited by zero on one end.

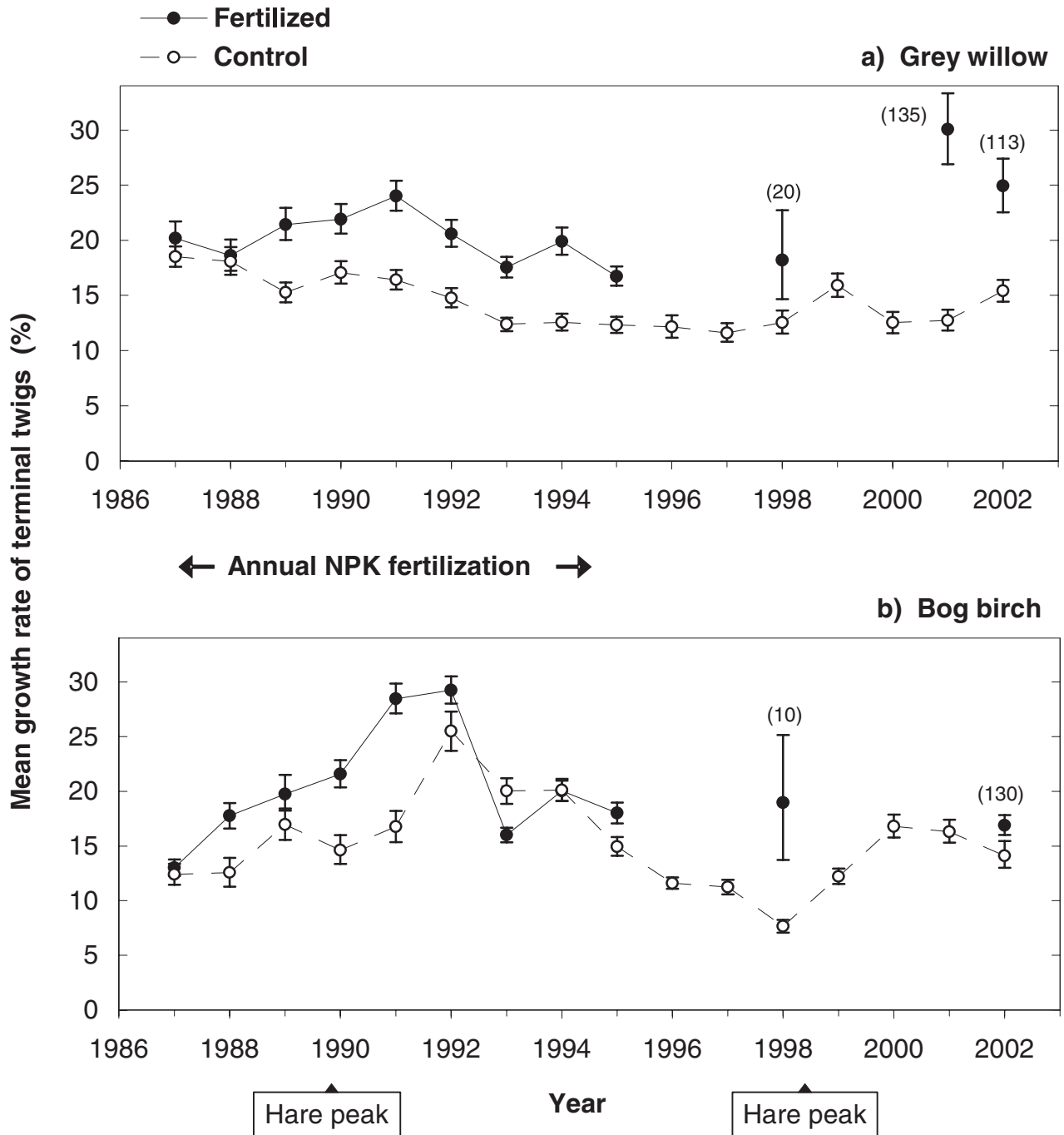
Analysis of variance (ANOVA) was used to compare growth rates between treatments and years, with plots nested within treatments. Only post-fertilization years when both control and fertilized twigs were sampled were considered (willow: 1998, 2001, 2002; birch: 1998, 2002). Two measures of growth were independently tested: the growth rate index and biomass of the current annual growth. Both measures were transformed for normality; willow data were log-transformed and birch data were square-root transformed. Tukey's HSD 95% confidence intervals were calculated for post-hoc comparison of means. All intervals given in this paper are for 95% confidence limits.

To measure N concentration in 1998, we sampled willow twigs on two plots and birch twigs on one plot in May 1999 before the start of the growing season. Twigs were dried at 60 °C for 4 d, then re-dried 4 months later prior to measuring N concentration. The 1998 growth tissue was ground to 0.5 mm with a Wiley mill prior to analysis of total N concentration using the Kjeldahl method (Bremner 1996). Lumping of individual twigs was necessary to provide enough mass for analysis; twigs were randomly paired within plots for a sample size of five twig pairs per plot for each species. Willow samples were pooled within control plots and fertilized plots since neither variances nor means differed within treatments at $\alpha = 0.05$ when we used an *F* variance ratio test or 2-tailed *t* test with pooled variance, respectively. To compare N concentration between fertilized and control plots, we used 2-tailed *t* tests assuming unequal variances because variances were significantly different at $\alpha = 0.05$ for both willow and birch, using an *F* test. We calculated N content (= 1998 dry weight × N concentration) as another measure of tissue nitrogen level to compare between control and previously fertilized twigs.

Results

During the period between 1987 and 1994 when fertilizer was added, annual growth rates of grey willow shrubs were, on average, 33% higher on fertilized plots than on control

Fig. 1. Growth rate of 5-mm-diameter twigs between 1987 and 2002 for grey willow (*Salix glauca*) (a) and bog birch (*Betula glandulosa*) (b). Average sample sizes of control and fertilized twigs between 1987 and 1995 were 540 for willow and 338 for birch. Average sample sizes on control plots between 1996 and 2002 were 421 for willow and 235 for birch. Sample sizes for fertilized twigs in 1998, 2001, and 2002 are indicated beside the data points. Bootstrapped means and 95% confidence limits are shown. Years of peak snowshoe hare abundance are indicated.



plots (i.e., the ratio of fertilized to control data was 1.33), while those of birch were 22% higher on fertilized plots (Fig. 1). Several years after NPK fertilization stopped, residual effects on growth were observed in both willow and birch. The effect of the fertilizer treatment varied between years; willow and birch both showed a highly significant treatment × year interaction in growth rate ($p = 0.001$, Table 1). The interaction was similar when biomass of current

annual growth was analyzed instead of the growth rate index (Table 1).

The growth rate of fertilized grey willow shrubs (18.2%, 95% confidence limits of 14.7%–22.7%) was higher than that of the control shrubs (12.5%, 11.5%–13.6%) in 1998 (Tukey’s HSD, $p < 0.05$; Fig. 1a). When we resampled willows in 2001 and 2002, willows in the previously fertilized areas showed even higher growth rates (average 2001 and

Table 1. ANOVA results for willow and birch growth data from control and previously fertilized plots.

| Source of variation | df | Growth rate index | | | Biomass of new growth | | |
|--|------|-------------------|----------|----------|-----------------------|----------|----------|
| | | MS | <i>F</i> | <i>p</i> | MS | <i>F</i> | <i>p</i> |
| Grey willow (log-transformed) | | | | | | | |
| Treatment | 1 | 22.50 | 283.14 | <0.001 | 13.57 | 132.58 | <0.001 |
| Year | 2 | 1.36 | 17.08 | <0.001 | 0.04 | 0.34 | 0.710 |
| Treatment × plot | 2 | 0.12 | 1.56 | 0.210 | 0.01 | 0.09 | 0.913 |
| Treatment × year | 2 | 0.54 | 6.73 | 0.001 | 0.92 | 8.97 | <0.001 |
| Treatment × plot × year | 4 | 0.12 | 1.55 | 0.184 | 0.07 | 0.67 | 0.612 |
| Residuals | 1558 | 0.08 | | | 0.10 | | |
| Bog birch (square root-transformed) | | | | | | | |
| Treatment | 1 | 91.19 | 141.55 | <0.001 | 0.64 | 17.88 | <0.001 |
| Year | 1 | 91.56 | 142.12 | <0.001 | 0.76 | 21.30 | <0.001 |
| Treatment × plot | 1 | 1.24 | 1.92 | 0.167 | 0.01 | 0.19 | 0.663 |
| Treatment × year | 1 | 15.96 | 24.78 | <0.001 | 1.27 | 35.31 | <0.001 |
| Residuals | 548 | 0.64 | | | 0.04 | | |

Note: Willow data are from 1998, 2001, and 2002; birch data are from 1998 and 2002.

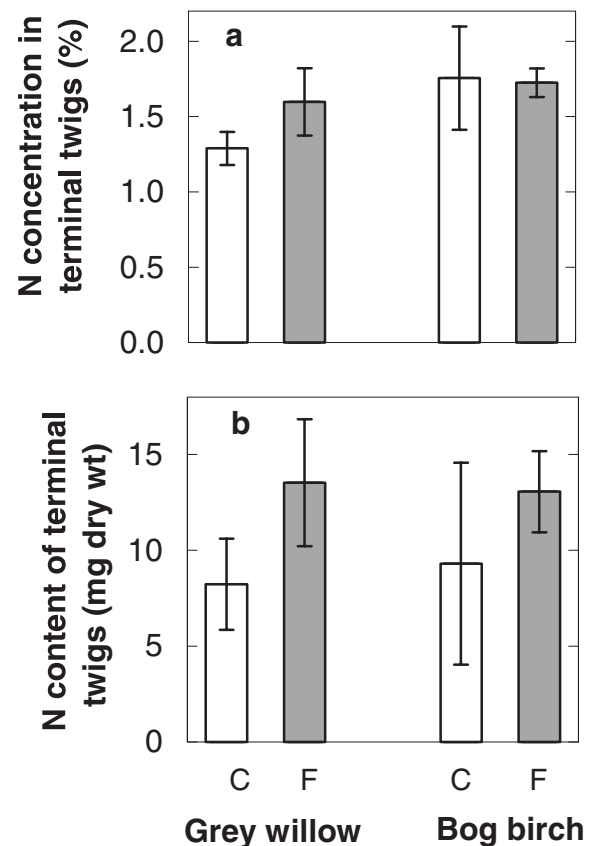
2002, 27.5%, 24.7%–30.4%) relative to twigs on the control areas (14.1%, 13.1%–15.1%), a highly significant effect on growth rate 7–8 years after fertilization had ended (Tukey's HSD, $p < 0.001$; Fig. 1a).

Birch growth rates were more strongly influenced by the snowshoe hare cycle, tending to reach a peak on control plots about 2–3 years after the snowshoe hare population peak had passed (Fig. 1b). Hares reached peak densities in the Kluane region in 1989–1990, and again in 1998 (Krebs et al. 2001). Growth rates of control shrubs were negatively correlated with hare abundance between 1987 and 2002 (Pearson's $r = 0.66$, $t_{14} = 3.27$, $p = 0.003$; hare data from C. Krebs, Kluane Monitoring Program, not shown). The growth rate of fertilized birch shrubs (19.0%, 13.7%–25.2%) was higher than control shrubs (7.7%, 7.1%–8.2%) in 1998 (Tukey's HSD, $p < 0.05$; Fig. 1b). In contrast to willow, the growth rate of previously fertilized birch shrubs (16.9%, 16.0%–17.8%) returned nearer to control levels (14.1%, 13.0%–15.5%; Tukey's HSD, $p > 0.05$) by 2002 during lower hare abundance (Fig. 1b).

Neither willow nor birch showed a plot effect (treatment × plot interaction terms, $p > 0.15$, Table 1). The greatest discrepancy between measures of growth occurred in willow, where an overall year effect was observed for the growth rate index but not for biomass of new growth (Table 1) because 5-mm twig weights varied between years. Both species had a highly significant overall treatment effect 4–8 years after fertilization ended, regardless of which measure of growth was used ($p < 0.001$, Table 1).

Willow and birch also responded differently to fertilization in their 1998 tissue nitrogen levels. For willow, N concentration was greater in fertilized twigs (1.60%, 1.37%–1.82%) than control twigs (1.29%, 1.18%–1.40%; $t_{8,8} = 2.86$, $p = 0.013$; Fig. 2a), but for birch N concentration did not differ between control (1.75%, 1.41%–2.10%) and fertilized (1.72%, 1.63%–1.82%) twigs ($t_{4,4} = 0.21$, $p > 0.8$; Fig. 2a). Nitrogen content (Fig. 2b) was more variable than N concentration because of the added variation in dry weight. Coefficients of variation for N content were 33%,

Fig. 2. Nitrogen concentration (% of dry weight) (a) and total N content (mg dry weight) (b) of terminal twigs from the 1998 growing season for grey willow and bog birch on control (C) and fertilized (F) plots. Twigs were clipped in May 1999 before growth began. Plant tissue was pooled for the analysis; sample size is five twig pairs per plot, with willow sampled on two plots and birch on one plot. Error bars are 95% confidence limits.



35%, 50%, and 11% for willow control, willow fertilized, birch control, and birch fertilized, respectively, while for N concentration they were only 12%, 18%, 16%, and 3%, respectively.

Discussion

Growth rates of willow and birch shrubs from 1988 to 1994 generally increased in response to long-term fertilization (Turkington et al. 1998; Fig. 1). Since 1994 when fertilization ceased, growth and N level responses have been different for willow and birch when control and previously fertilized shrubs are compared. Because shrub growth rates vary during the snowshoe hare cycle, especially for birch, we compared our results from the growing seasons of 1998, 2001, and 2002 after fertilization ceased to those from 1990, 1993, and 1994, the years during fertilization with comparable levels of hare abundance.

The residual effects of fertilization on willow growth were strong. In all years since 1989, growth rates of fertilized willow shrubs consistently remained above those of control shrubs (Fig. 1a). Growth rates of fertilized shrubs were 28%, 42%, and 58% higher than those of control shrubs in 1990, 1993, and 1994, respectively, during fertilization. Ratios between fertilized and control shrubs expanded even more after fertilization had ceased, with growth rates of fertilized willow shrubs 45%, 136%, and 62% higher than those of control shrubs in 1998, 2001, and 2002, respectively, the equivalent years of the snowshoe hare cycle (Fig. 1a). The greater differences observed after fertilization had ceased suggest that residual effects of long-term fertilization can be greater than short-term effects (e.g., Milchunas and Lauenroth 1995), most likely because of the storage and subsequent recycling of nutrients in shrub biomass in the boreal forest.

The residual effects of fertilization were also evident for willow in its N levels. In 1990, N concentration of fertilized willow twigs (1.23%, 1.19%–1.27%) was 34% higher than that of control twigs (0.91%, 0.89%–0.93%) (Sinclair et al. 2001). In 1998, N concentration in the new tissue of previously fertilized willow twigs was still 24% higher than control twigs (Fig. 2a). Long-term, persisting N concentration increases have been observed in other systems, such as in grasses and half-shrubs of shortgrass steppe communities, where N concentration of above-ground plant tissue remained higher in N fertilizer treatments than controls 20 years after fertilization ended (Vinton and Burke 1995). Willow twigs had higher N concentration in 1998 than in 1990 on both control and fertilized plots, indicating year-to-year variability in tissue N levels.

In contrast to willow, birch growth seemed to depend on hare browsing, as growth rates of control shrubs were negatively correlated with hare abundance. Birch growth on control plots tended to be highest during the declining and low phases of the cycle, and lowest during the increasing and peak phases. During the hare peak, fertilized shrubs had higher growth rates than control shrubs (1990 during fertilization, 47% higher; 1998 after fertilization, 148% higher). At low hare abundance, there appears to be little difference in growth rate between control and fertilized birch shrubs

(Fig. 1b, 1994 and 2002). Birch shrubs are the preferred winter food for hares and are heavily browsed during the hare peak, with hares typically eating 90% of all birch branches at the peak in contrast to only 20%–30% of willow branches. This may slow birch growth rates during the hare peak on control plots, but less so on fertilized plots where additional nutrients maintain high growth rates despite heavy browsing. Unfortunately, since adequate 1998 birch samples were present on only one fertilized area, we are unsure whether the large difference in growth rate during the hare peak would hold if replicated. If residual effects of fertilizer on birch growth have disappeared, we expect growth rates on control and previously fertilized areas to remain similar in future years, including the upcoming hare peak.

During the hare peak of 1998, the higher growth rate (Fig. 1a) and higher N concentration (Fig. 2a) of willow on fertilized plots suggests greater availability of high-protein food for snowshoe hares and other herbivores (Sinclair et al. 1982, 2001). Similarly, the higher growth rate of birch on fertilized plots in 1998 (Fig. 1b) suggests an increased availability of this shrub, which hares prefer (Krebs et al. 2001). Evidence for bottom-up effects was seen in 1989–1990, the previous peak of herbivore biomass: fertilization was observed to increase herbivory (Sinclair et al. 2000), which in turn resulted in 85% higher hare biomass on fertilized plots than on control plots. The continued improvement of willow and birch forage on the previously fertilized plots was shown by heavy winter moose browsing on these sites in the six winters of 1998–2004 (C. Krebs, personal observations), an indication that the differences in forage quality were biologically relevant.

The proportional distribution of the added nutrients from fertilization remains unknown. Some nutrients have likely leached out of the ecosystem, a large proportion is probably within the soil in immobile forms (Binkley 1986), and another proportion has likely been retained in compartments of the plant community. Our observed responses to fertilization suggest that some of the added nutrients were in shrubs 4–8 years after fertilization stopped. White spruce is also a potential nutrient sink, as N is often recycled within trees in N-limited systems (Miller 1988). During fertilization, the herbaceous vegetation responded to added nutrients with an increase in total biomass (Turkington et al. 1998). Nutrients return to the humus annually when these herbs die, or when shrubs and trees die or lose foliage. Plant increases in biomass, growth rate, or tissue nutrient concentration resulting from fertilization should eventually generate more litter or higher-nutrient litter that subsequently decomposes, which is obviously possible for several years after fertilization (Prescott et al. 1995). The most likely mechanism for the observed residual effects of fertilization on shrub growth is storage and recycling of added nutrients. It is supported for two reasons: (i) the heavily grazed birch twigs showed less of a growth response than the less heavily grazed willow twigs, and recovery from grazing would have presumably depleted within-plant nutrient stores in birch; and (ii) N concentration in the new tissue of fertilized willow twigs was higher than control twigs.

The data presented here show continuing growth and nutrient differences in shrubs 4–8 years after fertilization

stopped and suggest that it would be useful to do a complete nutrient budget for this northern boreal forest region, particularly for nitrogen. The use of fertilizer isotopes (e.g., Preston et al. 1990) would allow us to measure the rate of cycling of added nutrients, trace where they end up in the system several years after fertilization, and assess their effects on plant productivity.

The pulsed disturbance of nutrient enrichment on ecosystems may lead to long-term effects that are qualitatively different from and unpredictable from the immediate effects of enrichment (Milchunas and Lauenroth 1995). The large growth responses we observed in willow 7–8 years after fertilization stopped could not have been easily predicted from the responses observed during the treatment. Continued monitoring of shrub growth and N concentration on these previously fertilized plots will allow us to assess the decay curves and total number of years before the residual effects from fertilization approach control levels.

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