

The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study

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Summary

1 The influence of fertilizer addition and mammalian herbivore exclosures (a 2×2 factorial design, with four replicates at each of two sites) on the cover, species composition and diversity of the understorey vegetation of the boreal forest in the south-western Yukon, Canada, were investigated from 1990 to 1999. This was done to test whether vegetation composition was controlled by resource level alone (bottom-up control), herbivory alone (top-down control), or by both (interactive control).

2 The density of the major herbivore, the snowshoe hare, varied 25-fold, declining from 148 km^{-2} in 1990 to 8 km^{-2} in 1994, and increasing to a second peak of 198 km^{-2} in 1998.

3 In control plots most species were remarkably constant in percent cover. After 10 years, most of the major species showed significant responses to fertilizer with four species increasing (*Festuca altaica*, *Mertensia paniculata*, *Epilobium angustifolium*, and *Achillea millefolium*), and three declining (*Linnaea borealis*, *Lupinus arcticus*, *Arctostaphylos uva-ursi*). Some species took up to 5 years before a response was detected.

4 Fertilization caused (i) a decline in the number of species, and species evenness in the community, (ii) a reduction in the proportion of woody species, and (iii) an increase in herbaceous dicotyledons and grasses.

5 The exclusion of herbivores had virtually no impact on the abundance of the vegetation or on species diversity, except in 1990–92 during a decline from a peak of 148 hares km^{-2} to 29 hares km^{-2} .

6 These results suggest that the percentage cover and composition of herbaceous vegetation in the boreal forest are determined almost exclusively by the productivity of the site (bottom-up control) and that the activities of mammalian herbivores may be important only during peaks in hare population densities (interactive control).

7 Results were both species-specific and time-dependent, suggesting that long-term studies are needed to discriminate between long-term responses to treatments and transient phenomena.

Key-words: boreal forest, bottom-up, dominance–diversity plots, nutrient addition, snowshoe hare cycle, species diversity, top-down

Journal of Ecology (2002) **90**, 000–000

Introduction

Much research effort has been focused on the relative roles of nutrient level and herbivores in regulating vegetation abundance (e.g. Pastor & Naiman 1992;

Power 1992; John & Turkington 1995); the so-called 'bottom-up' and 'top-down' controls on plant productivity. Herbaceous plants growing in the understorey of the boreal forest have to contend with moderately stressful conditions characterized by low levels of light filtering through the canopy, prolonged periods of low winter temperatures coupled with brief, cool growing seasons and cold soils with low fertility and, often, low

moisture. In addition, approximately every 10 years throughout most of the boreal forest of North America, plants are subjected to elevated levels of snowshoe hare grazing as the hares reach peak population densities (up to 300 km⁻², Krebs *et al.* 1986) during their population cycle. The understory vegetation is the primary source of food for mammalian herbivores during the snow-free season (Seccombe-Hett 1999) and it is therefore important to understand the factors that influence and regulate growth of these plants.

Soil nutrients, especially nitrogen, often limit the productivity of boreal forest vegetation (Bonan & Shugart 1989; Nams *et al.* 1993; Turkington *et al.* 1998), and may control species abundances. Plants differ in their abilities to respond to raised nutrient levels, and community composition usually changes following fertilization as different species begin to dominate. In many habitats species richness, diversity or evenness decline when nutrient supply is enhanced (e.g. Gerhardt & Kellner 1986; Tilman 1987b; Dirkse & van Dobben 1989; Rajaniemi 2002). This is probably due to the ability of superior competitors for light to dominate the community when nutrient levels are raised. In addition, herbivory has long been known to influence species composition in some plant communities (Huntly 1991) due to species differences in palatability and ability to tolerate herbivory. Herbivory often contributes to the maintenance of diversity, by preventing potential dominants from competitively eliminating other species (Huntly 1991) **1** The snowshoe hare has distinct preferences among the summer forage species available in the boreal forest (Seccombe-Hett 1999).

We tested whether the herbaceous plant community as a whole is limited primarily by nutrient availability, by herbivory, or by their interaction by monitoring how fertilization and the exclusion of major herbivores influenced individual species' abundance and thus community composition. In the so-called bottom-up or resource-control hypothesis it is assumed that systems are regulated by nutrient flow from below; higher trophic levels (in our case herbivores) have no regulating effect on productivity or biomass on the levels below them (McNaughton *et al.* 1989; Hunter & Price 1992). Conversely the 'top-down' or consumer-control hypothesis assumes that top predators are self-regulating and each level then regulates the level below (Menge & Sutherland 1976), and the plants are limited by herbivore, rather than nutrient, levels. Many other models involve variations of the top-down and/or bottom-up hypotheses (e.g. Oksanen *et al.* 1981; Carpenter *et al.* 1985; Fretwell 1987; Oksanen 1990). **2**

We imposed fertilization in the presence and absence of herbivore exclusion, treatments that allow us to make specific predictions about changes in vegetation abundance (estimated as percentage cover), and changes in species number and diversity, under three different hypotheses.

HYPOTHESIS 1: VEGETATION IS CONTROLLED BY NUTRIENT AVAILABILITY ALONE (BOTTOM-UP, OR RESOURCE CONTROL)

This hypothesis leads to four predictions.

1. There will be an overall increase in the abundance of vegetation in fertilized plots.
2. Herbivore exclusion alone will not lead to an increase in vegetation abundance.
3. Community composition will change in response to fertilization according to species differences in the ability to respond to raised nutrient levels. Specifically we predict that grasses and most of the taller herbaceous dicotyledons will increase, whereas prostrate species and groups such as woody vines, mosses, and lichens will decline.
4. Species number and diversity will decline in fertilized plots because of increasing dominance by a few species.

HYPOTHESIS 2: VEGETATION IS CONTROLLED BY HERBIVORES ALONE (TOP-DOWN OR CONSUMER CONTROL)

This hypothesis leads to three predictions.

1. There will be no increase in vegetation abundance when plots are fertilized but unfenced.
2. Vegetation abundance will increase in exclosures.
3. Species number and diversity will decline inside exclosures because removal of herbivores will permit competitively dominant plant species to exclude some less competitive species.

HYPOTHESIS 3: VEGETATION IS CONTROLLED BY BOTH NUTRIENT AVAILABILITY AND HERBIVORY (INTERACTION CONTROL)

This hypothesis leads to three predictions.

1. There will be an increase in plant growth in fertilized plots but there will be an interaction between the exclosure and fertilizer treatments as herbivores remove some of the additional growth due to fertilizer.
2. In herbivore exclosures, vegetation abundance will increase.
3. Plots that have been both fertilized and fenced will have the lowest species number and diversity because both treatments lead to the exclusion of some plant species.

Short-term studies can never substitute completely for direct long-term observations of ecological phenomena and they may produce misleading results if, for example, the effects of herbivory on the herbaceous vegetation were studied only during a low phase of the herbivore population cycle. In addition, it is important to determine whether initial community changes in response to treatments are transient (*sensu* Tilman 1988) and to determine the length of time required to produce more permanent shifts in vegetation abundance and composition. There are numerous examples of the central role of long-term studies (Franklin 1987; Likens 1987; Tilman 1987a). They are particularly

valuable when investigating slow processes and rare or episodic phenomena (Franklin 1987): the boreal forest provides both and this study is therefore continuing after initially being run for 10 years.

Our previous study (John & Turkington 1995) monitored vegetation responses to fertilization and exclosures during the decline phase of the snowshoe hare cycle: here we focus more on the long-term responses of plant species to the treatments and place additional emphasis on the consequences for community diversity.

Materials and methods

THE STUDY AREA

The study area is near Kluane Lake in the Shakwak Trench, a wide glacial valley in the south-western Yukon in northern Canada, and is described by John & Turkington (1995, 1997), Turkington *et al.* (1998) and Krebs *et al.* (2001a). The area is in the rain shadow of the St. Elias Mountains and receives a mean annual precipitation of *c.* 230 mm, mostly falling as rain during the summer months, but including an average annual snowfall of about 100 cm. The forest in the region is patchy as a result of fire history. Over the past 200 years there have been relatively few large fires and a high frequency of small fires (Francis 1996; Dale *et al.* 2001). The region is a closed to open spruce forest community and the dominant tree is white spruce (*Picea glauca* (Moench) Voss), interspersed with stands of trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The understorey is dominated by shrub willows (*Salix glauca* (L.) and other *Salix* spp.), dwarf birch (*Betula glandulosa* Michx.), soapberry (*Shepherdia canadensis* (L.) Nutt.), and a well developed ground layer, chiefly arctic lupine (*Lupinus arcticus* S. Wats.), northern rough fescue (*Festuca altaica* Torr.), twin flower (*Linnaea borealis* L.), bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), bluebells (*Mertensia paniculata* (Aiton) G. Don), and yarrow (*Achillea millefolium* L. var. *borealis* (Bong.) Farwell). Snowshoe hares (*Lepus americanus* Erxleben) are the primary herbivore and they undergo a regular 10–12-year cycle. Hares were at peak densities of 148 km⁻² in 1990, declined to 8 km⁻² in 1994 (Boutin *et al.* 1995; Krebs *et al.* 1995), and increased to a second peak of 198 km⁻² in 1998 (Hodges *et al.* 2001). Many other small mammals include herbaceous vegetation in their diet but these were quite infrequent at our sites. The first major impacts of an outbreak of spruce bark beetle were observed in 1995 and, as mature trees die and the canopy becomes more open, increased light penetration will undoubtedly influence processes at ground level.

EXPERIMENTAL DESIGN

This experiment was replicated at two sites in areas of moderately open spruce forest (45–60% canopy cover,

typically 160–220 stems/ha) with a well developed (> 90% cover) herbaceous understorey, the first approximately 2 km to the south of Boutellier summit on the Alaska highway and the second 50 m to the north of Boutellier summit at km 1695 on the Alaska highway (61°02' N, 138°22' W). Both sites were probably last burned in 1872 (Francis 1996; Dale *et al.* 2001). Details of the sites and design are provided by John & Turkington (1995, 1997). Sixteen 5 m × 5 m plots were selected in small meadows at each site. None of the plots had any rooted trees and only a few had scattered shrubs, most of which were less than 1 m tall. At each site, the plots were randomly divided among four treatments: control (no treatment), fence only, fertilizer only, and fence with fertilizer. Fences were 1 m high and made of galvanized chicken wire with 2.5 cm mesh, supported by 2 m steel T-bars, and firmly stapled to the ground to prevent animals intruding under the fence; there was no obvious evidence of any herbivory inside fenced plots. Fertilizer (N:P:K 35 : 10 : 5) was applied in granular form each year between mid-May and early June after snow melt at a rate of 1.25 kg per 5 m × 5 m plot per year, resulting in an addition of 17.5 g N/m²/year, 5 g P/m²/year and 2.5 g K/m²/year. Natural mineralization rates in white spruce forests are about 4.7 g N/m²/year (Binkley & Hart 1989). This application rate was used to be consistent with other studies being done in our area (Boutin *et al.* 2001 p. 60) and is within the range used in other long-term fertilization experiments (Weetman & Fournier 1984; Tamm 1985; Kellner 1993). Because many boreal forest herbs are clonal the soil was cut annually, in early June, to a depth of 20 cm around each plot, to sever rhizomes that could connect plants inside and outside each plot.

Because of the on-going nature of the project we could not use destructive sampling procedures and therefore percentage cover was measured to represent abundance. Pre-treatment measurements were made in early June 1990 and then measurements made in early August each year from 1990 to 1999. In each plot, the species present (less than 1 m tall) were recorded every 10 cm along five 4-m long transects. Percentage cover for each species was the percentage of points (out of 205) at which the species was present. All mosses were recorded in a single category. The lichen genus *Peltigera* was also placed in a single category, but consisted mostly of the nitrogen-fixing species, *Peltigera canina*.

DATA ANALYSES

The experimental design was four replicates of four factorial treatments (± fertilizer × ± fencing) in each of two blocks (i.e. sites). Data were analysed over years by Repeated Measures ANOVA (von Ende 1993). Standard tests of the main and interaction effects of years do not allow for the quantitative nature of years in that they indicate the inequality of the effects but not the nature of the inequality. Instead, the effects were further subdivided into two contrasts and tested. The contrasts were for a

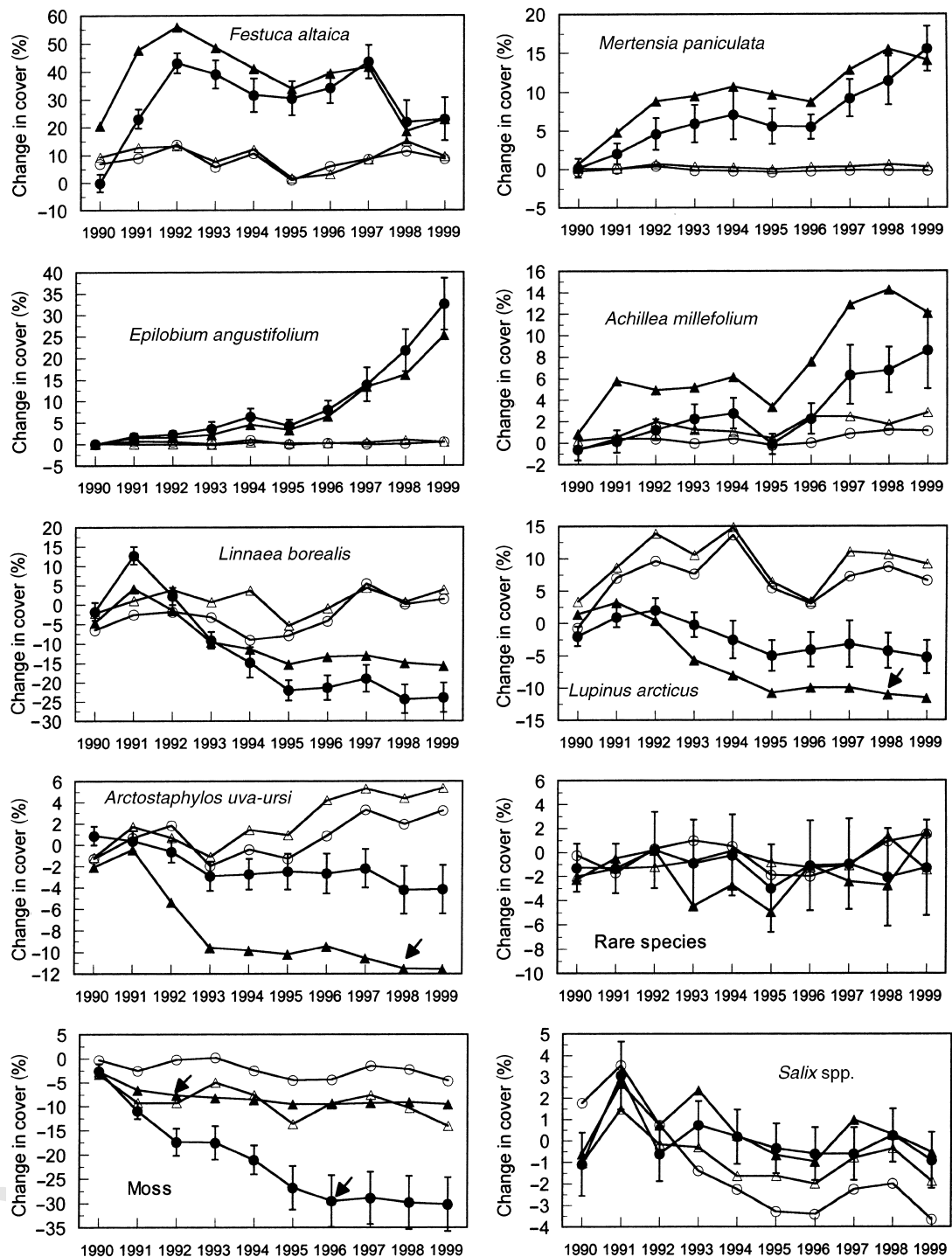


Fig. 1 Change in percentage cover for species from a boreal forest in north-western Canada in response to treatments. Differences in percentage cover in 1990 represent changes that occurred between the pre-treatment survey in early June 1990 and the first post-treatment survey in early August 1990. Arrows indicate the point at which a species in a particular treatment had reached 0% cover (i.e. absent) and can therefore decline no further; (for *Mertensia* and *Epilobium* this applies throughout both unfertilized treatments). Solid symbols show fertilized treatments, open symbols unfertilized. Triangles show fenced treatments, circles unfenced. Error bars are ± 1 SE, and, because the analysis assumes that the error variance is the same for all treatments in a year for a species, are presented for just the one treatment.

linear, or straight line effect and for variation about the straight line, which in this context is referred to as a non-linear effect. This allowed the determination of whether the main and interaction effects of years followed a mainly linear trend or whether other trends were evident. Data were also analysed for each year in

turn for the main effects of fertilizer and fencing and their interaction. This analysis was by ANCOVA (Payne *et al.* 1993) using data from a pre-treatment survey in 1990 as the co-variate. The co-variate was significant ($P < 0.05$) in 88 of 100 cases (10 species \times 10 years). For clarity the data have been plotted (Fig. 1) as

Table 1 The actual percentage cover of nine abundant taxa in the boreal forest of north-western Canada, and all other species combined (rare species) in the four treatments in the first survey in June 1990 and in the final survey in August 1999

Plant species or group	Not fertilized				Fertilizer added			
	Not fenced		Fenced		Not fenced		Fenced	
	1990	1999	1990	1999	1990	1999	1990	1999
<i>Achillea millefolium</i>	0.1	3.6	2.0	7.4	0.5	19.4	5.9	28.9
<i>Arctostaphylos uva-ursi</i>	19.0	28.3	15.3	28.6	11.4	1.1	20.8	1.3
<i>Epilobium angustifolium</i>	0.8	1.5	0.5	1.1	0.4	67.3	1.4	53.3
<i>Festuca altaica</i>	41.8	45.3	59.8	60.1	34.4	81.5	82.4	87.1
<i>Linnaea borealis</i>	46.5	62.8	35.8	48.1	51.5	6.1	24.0	1.4
<i>Lupinus arcticus</i>	25.8	40.8	32.0	44.0	8.9	2.3	28.4	1.8
<i>Mertensia paniculata</i>	0.3	0.4	0.4	0.8	1.0	32.5	3.0	30.5
Moss	14.0	5.1	31.9	9.9	57.0	0.4	13.9	0.0
<i>Salix</i> spp.	13.0	1.9	3.9	2.1	4.4	4.8	6.1	6.3
Rare species	19.0	36.1	19.9	31.8	17.6	15.0	33.5	27.0
Total	180.1	225.6	201.3	233.9	187.0	230.3	219.3	237.4

a change in percentage cover from the initial post-treatment survey with error bars from the analysis of the changes in percents.

The abundances of the most prevalent species were analysed as data variables. Species with less than 1.5% cover averaged over all 32 plots for all 10 years were grouped into a single category called rare species.¹ Such percentage cover values were angular (i.e. arcsin square root) transformed before analysis to normalize the data and to homogenize the variance.

Dominance–diversity graphs were prepared by plotting species abundance against species rank for each plot in each year. To test for consistent effects of the treatments on the dominance–diversity of the plots, the slopes of straight lines fitted to each plot's graph were analysed.

To determine whether there were consistent effects of time or treatments on the species composition of the plots, the species evenness of each plot was assessed. Many evenness indices have been proposed and the choice of a suitable index has become a problem. Smith & Wilson (1996) assemble many criteria for an appropriate index and argue that the most important criterion is that evenness should be independent of species richness. On this basis, the overall recommendation for general use is Smith & Wilson's (1996) E_{var} (programmed in Krebs 1999) which is calculated using:

$$E_{\text{var}} = 1 - 2/\pi \arctan \left\{ \frac{1}{S} \sum_{r=1}^S \left[\ln(x_r) - \frac{\sum_{r=1}^S \ln(x_r)}{S} \right]^2 \right\}$$

where x_r is the abundance of the r th species on the plot, and $r = 1, \dots, S$, where S is the number of species.

Results

Although this boreal forest understorey community is quite species-rich, with up to 30 plant species in some of the 5 m × 5 m plots, most of these species are infrequent and are therefore included within the rare species category. Only nine taxa typically comprised more than 1.5% cover, and four of these (*Arctostaphylos*, *Festuca*, *Linnaea* and *Lupinus*) had consistently greater than 10% cover (Table 1). In control plots, *Salix* spp. (chiefly *S. glauca*) and mosses were the only ones to show a decline; the other species remained constant (*Mertensia*, *Epilobium*) or had substantial increases in their abundance over the 10-year period (Table 1, Fig. 1).

SPECIES RESPONSES TO FERTILIZER

Most species except moss, *Salix* spp. and the 'rare species' showed significant responses to fertilizer after 10 years (Tables 1 and 2; Fig. 1). The cover of four species increased relative to controls (*Festuca altaica*, *Mertensia paniculata*, *Epilobium angustifolium*, and *Achillea millefolium*), and three declined (*Linnaea borealis*, *Lupinus arcticus*, *Arctostaphylos uva-ursi*). Although the change in percentage cover for some species was quite marked, the net changes in total percentage cover of all species in response to the treatments was rather limited (Table 1).

¹ The category 'Rare species' includes the following: *Anemone multifida*, *Anemone parviflora*, *Arctostaphylos rubra*, *Arnica cordifolia*, *Aster sibiricus*, *Betula glandulosa*, *Calamagrostis purpurescens*, *Castilleja* spp., *Cornus canadensis*, *Delphinium glaucum*, *Elymus repens*, *Empetrum nigrum*, *Hedysarum alpinum*, *Moneses uniflora*, *Orthilia secunda*, *Pedicularis sudetica*, *Penstemon procerus*, *Picea glauca* (seedlings), *Polemonium acutiflorum*, *Senecio lugens*, *Shepherdia canadensis*, *Solidago multiradiata* and *S. simplex*, *Stellaria longipes*, *Zygadenus elegans*, and species of *Antennaria*, *Arabis*, *Astragalus*, *Carex*, *Cladonia*, *Equisetum* (mostly *E. scirpoides*), *Gentiana*, *Peltigera*, and *Selaginella* (nomenclature from Cody 1996).

Table 2 Results of Repeated Measures (over years) ANOVA performed on angular (arsin square root) transformed percentage cover of species testing the effects of fertilizer, herbivore exclusion (fence) and site in a boreal forest of north-western Canada. The strata refer to the source of error variation that the effects are compared with. Because the factor year has quantitative levels, its main and interaction effects are further subdivided into a contrast for a linear, or straight line effect and a contrast for variation about the straight line, referred to as a non-linear effect

Plant species or group	Site × Plot stratum			Site × Plot × Year stratum			Contrasts of Year effects										
	Ft	Fn	Ft × Fn	Y	Y × Ft	Y × Fn	Y × Ft × Fn	Y L	Y NL	Y L × Ft	Y NL × Ft	Y L × Fn	Y NL × Fn	Y L × Ft × Fn	Y NL × Ft × Fn	Y L × Ft × Fn	Y NL × Ft × Fn
<i>Festuca</i>	***	*	NS	***	***	NS	NS	NS	***	NS	***	**	NS	**	NS	**	NS
<i>Limnacia</i>	***	NS	NS	***	***	NS	NS	***	***	***	*	NS	NS	**	NS	**	NS
<i>Lupinus</i>	***	NS	NS	***	***	*	NS	***	***	***	**	***	NS	***	NS	***	NS
<i>Arctostaphylos</i>	***	NS	NS	***	***	*	NS	***	***	***	NS	***	NS	***	NS	***	NS
Moss	NS	NS	*	***	***	NS	NS	***	**	***	NS	***	NS	***	NS	***	NS
<i>Mertensia</i>	***	NS	NS	***	***	NS	NS	***	***	***	NS	NS	NS	**	NS	**	NS
<i>Epilobium</i>	***	NS	NS	***	***	NS	NS	***	NS	***	NS	NS	NS	NS	NS	NS	NS
<i>Salix</i>	NS	NS	NS	***	*	NS	NS	***	***	***	NS	NS	NS	*	NS	*	NS
<i>Achillea</i>	**	*	NS	***	**	NS	NS	***	***	***	NS	NS	NS	NS	NS	NS	NS
Rare species	NS	NS	NS	***	***	NS	NS	NS	***	***	NS	NS	NS	NS	NS	NS	NS

Abbreviations: Ft, fertilizer; Fn, fence; L, linear; NL, non-linear.
 *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, non-significant ($P > 0.05$).

Table 3 *F*-probability values from an Analysis of Covariance of angular (arcsin square root) transformed percentage cover data for species in a boreal forest of north-western Canada from 1990 to 1999, using data from a pre-treatment survey as the co-variate. Main effects (treatments) were fertilization of the plots, and the exclusion of herbivores (Fence effect). Snowshoe hare density data from Hodges *et al.* (2001)

Variable	Hare density/km ² Treatment	147.8 1990	86.5 1991	28.5 1992	8.3 1993	7.8 1994	18.3 1995	51.5 1996	75.9 1997	198.3 1998	132.5 1999
<i>Festuca</i>	Fertilizer	NS	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	NS	0.044
	Fence	< 0.001	0.006	0.048	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	< 0.001	0.040	NS	NS	NS	NS	NS	NS	NS	NS
<i>Linnaea</i>	Fertilizer	NS	< 0.001	NS	< 0.001	0.003	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	0.028	0.022	0.048	NS	NS	NS	NS	NS	NS	NS
<i>Lupinus</i>	Fertilizer	NS	0.011	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	Fence	0.009	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>Arctostaphylos</i>	Fertilizer	NS	NS	0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	0.017	0.017	0.015	0.004	NS	NS
Moss	Fertilizer	NS	NS	< 0.001	< 0.001	< 0.001	0.002	< 0.001	< 0.001	< 0.001	0.004
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>Mertensia</i>	Fertilizer	NS	0.002	0.002	< 0.001	0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	Fence	0.033	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>Epilobium</i>	Fertilizer	NS	NS	NS	NS	NS	0.006	0.002	0.002	< 0.001	< 0.001
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	0.028	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>Salix</i>	Fertilizer	NS	NS	NS	0.009	0.019	0.008	0.010	NS	0.016	NS
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>Achillea</i>	Fertilizer	NS	NS	NS	NS	0.022	NS	0.027	0.002	NS	0.013
	Fence	0.021	NS	NS	NS	NS	0.016	0.036	NS	NS	NS
	Fert × Fence	0.033	0.011	NS	NS	NS	NS	NS	NS	NS	NS
Rare	Fertilizer	NS	NS	NS	NS	0.005	0.033	NS	0.039	0.001	NS
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Regression	Fertilizer	NS	NS	NS	0.010	0.036	0.012	0.020	NS	< 0.001	0.012
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
<i>E_{var}</i>	Fertilizer	NS	NS	< 0.001	< 0.001	0.002	0.001	0.001	0.009	< 0.001	0.002
	Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Fert × Fence	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Although most species eventually responded to fertilization, the responses did not always become apparent until several years of treatment. For example, *Festuca*, *Linnaea*, *Lupinus* and *Mertensia* all showed a significant response to fertilizer the year following the initial treatment, *Arctostaphylos* and moss after 2 years, *Salix* 3 years, *Achillea* 4 years and *Epilobium* 5 years (Table 3). The repeated measures analysis indicated that overall there was a strongly linear year effect in all species, but that there was also a non-linear year effect possibly because the treatments took more than a year to show an effect. The effect of fertilizer changed linearly with years for all species except in *Festuca* (Table 2).

SPECIES RESPONSES TO HERBIVORE EXCLUSION

Throughout the 10 field seasons there were few fence effects or fence × fertilizer effects, although six of the nine species (all except *Arctostaphylos*, *Salix* and moss) had either a significant fence or fence × fertilizer effect in 1990, when hares were at a high of 148 km⁻² (Table 3). Only *Festuca*, *Linnaea*, *Arctostaphylos* and *Achillea* had a significant response in at least 3 of the 10 seasons (Table 3; Fig. 1) and, for *Festuca* and *Linnaea*, the two most abundant species, these occurred during or shortly after the peak in hare population density (1990–92). *Arctostaphylos* however, showed an effect

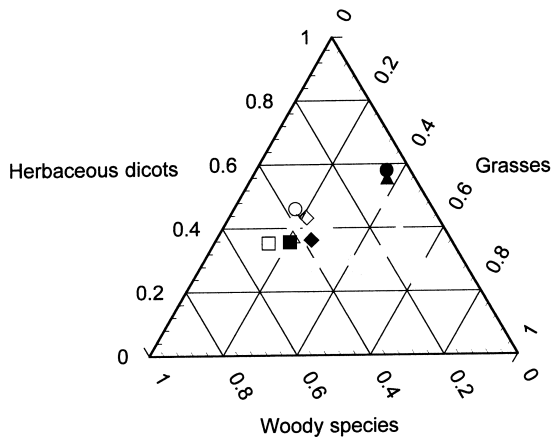


Fig. 2 Time course of relative abundance (estimated as percentage cover) of grasses, herbaceous dicotyledons (also includes mosses and lichens) and woody (*Linnaea*, *Arctostaphylos*, and shrubs) species in the boreal forest understorey. Pre-treatment composition in 1990 is an open symbol, 1991–98 are grey, and the final composition in August 1999 is dark. For fertilization and enclosures, \square (–), \diamond (–+), \circ (+–), \triangle (++).

during the hare low. During the first 5 years for *Festuca*, and throughout most of the experiment for *Achillea*, there was a greater increase in abundance in plots that were fertilized and fenced compared to those that were fertilized and unfenced, indicating that herbivores selectively ate fertilized plants when they were available. In all species except *Epilobium*, *Achillea* and rare species, there was either a fence effect that changed steadily with time or a fertilizer–fence interaction that changed steadily with time (Table 2).

COMMUNITY DIVERSITY RESPONSES TO FERTILIZER

There were major shifts in community structure caused by fertilization and this was largely driven by reductions in the percentage cover of the prostrate woody species (mostly *Linnaea* and *Arctostaphylos*), an increase in herbaceous dicotyledons (mostly *Mertensia*, *Achillea*, and *Epilobium*) and some increase in grasses (mostly *Festuca*) (Fig. 2). Fertilization caused a decline in both the number of species in the community (26.5 unfertilized vs. 18.5 fertilized; Fig. 3a) and the species evenness within those communities (Fig. 3b). A significant evenness response became apparent in 1992 (Table 3), two years after the initial application of fertilizer; again, the effect of fertilizer changed linearly with time. Fertilization resulted in an increasing dominance by some species in the community, and suppression of others, and resulted in shorter and steeper dominance–diversity plots (Fig. 4). In absolute terms, the largest and most immediate response to fertilization was by *Festuca* and, as *Festuca* increased, other species were excluded, species evenness declined (Fig. 3), and the slope of the rank–abundance plots increased ($P < 0.001$) (Fig. 4).

COMMUNITY DIVERSITY RESPONSES TO HERBIVORE EXCLUSION

Fenced and unfenced unfertilized plots remained relatively constant in their composition of growth forms (Fig. 2). There were no significant long-term community responses to the exclusion of herbivores either

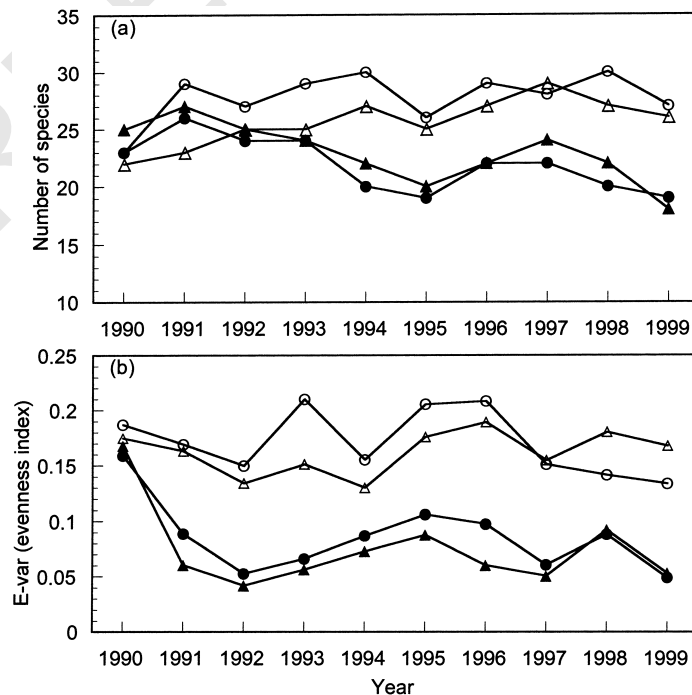


Fig. 3 (a) The number of species, and (b) evenness (calculated using the E_{var} equation of Smith & Wilson (1996)) of species from a boreal forest in north-western Canada, in plots subjected to treatments from 1990 to 1999. Solid symbols show fertilized treatments, open symbols unfertilized. Triangles show fenced treatments, circles unfenced.

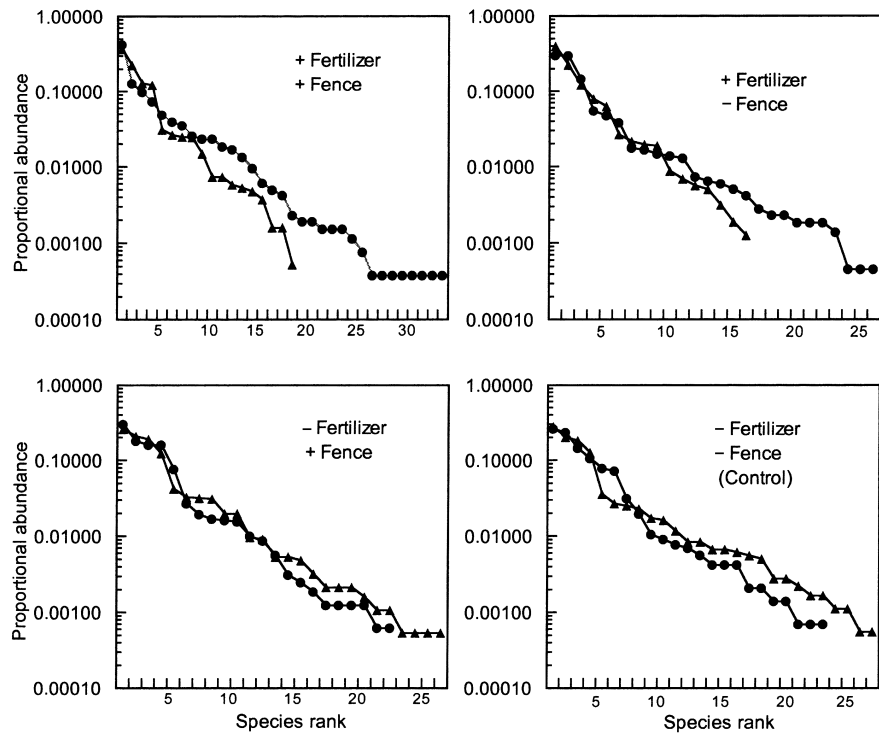


Fig. 4 Changes in patterns of relative abundance (estimated as percentage cover) of plant species in the boreal forest understorey when subjected to continuous treatments from 1990 (circles) to 1999 (triangles). Species are ranked in order of their abundance regardless of their identity.

in the number of species (Fig. 3a), or their evenness (Figs 3b and 4; Table 3).

Discussion

Our results generally support the hypothesis that the abundance of herbaceous vegetation is controlled by nutrient availability, i.e. bottom-up or resource-control. However, there is also evidence that herbivores were also partial determinants of vegetation abundance during the 1990–92 peak in snowshoe hare densities, i.e. interactive control, although this effect was not detected during the 1998–99 peak. The net changes in total percentage cover of all species in response to the treatments were rather limited and the most significant changes were reflected in the changing relative abundances of the species. However, although not measured in this study, there were visibly observable changes in the biomass of fertilized plots but not the fenced plots. These changes will be reported when a destructive harvest is made at the end of the study.

THE EFFECTS OF NUTRIENT AVAILABILITY ALONE (BOTTOM-UP CONTROL)

As predicted by the resource control hypothesis, fertilization resulted in an overall increase in the abundance of herbaceous vegetation, species number and diversity declined, vegetation composition changed, and vegetation abundance did not increase in the fence only treatments.

Many studies from a range of plant communities have shown that changes in fertility, primarily nitrogen, will alter species composition (Tilman 1987b; Bobbink 1991; Lepš 1999; Rajaniemi 2002). We predicted that those species that could respond most rapidly to the increased nitrogen would replace other less responsive ones. Understorey changes are common after nitrogen application to boreal forests (Gerhardt & Kellner 1986; Dirkse & van Dobben 1989); lichens and bryophytes typically decline (Kellner 1993), and grasses increase (Tamm 1991; Mäkipää 1995). The rapid and positive response of the grass, *F. altaica*, thus parallels results for graminoids in other northern ecosystems (Shaver & Chapin 1986). The strong positive response by some species to fertilizer addition is to be expected in a nutrient-limited system, although only four species (*Festuca*, *Mertensia*, *Epilobium* and *Achillea*) out of about 30, seem to have this ability. However, this community has evolved in low nutrient conditions and most wild plant species found in low productivity environments or infertile soils have inherently low relative growth rates (Chapin *et al.* 1986). This allows them to persist when nutrients are scarce, but they often lack the flexibility to respond to increased resources (Chapin *et al.* 1986). However, if one or a few species in the community are responsive, then the remainder become vulnerable to local extinction when nutrients are increased. In general, long-term fertilization caused a shift from a well-mixed community of grasses, prostrate woody species and herbaceous dicotyledons to a community dominated by tall, erect grasses and herbaceous

dicotyledons. The low-growing species probably suffered the consequences of light limitation by taller neighbours. Although we have not tested these interactions directly, it is quite likely that the strong growth responses exhibited by some species, particularly by *Festuca*, *Mertensia* and *Epilobium*, were directly or indirectly responsible for the decline of other species and the competitive exclusion of many, especially those that were already infrequent in the community. The decline in some species may however, also have been due to a direct effect of the fertilizer. Arie (1996) and Turkington *et al.* (2001) showed that even modest applications of fertilizer to populations of *Anemone parviflora*, in the absence of any neighbours, resulted in their decline but effects on other species have yet to be tested.

Early responses to fertilization were sometimes untypical of the longer term results, demonstrating the importance of continuing measurements. Some may even be misleading; for instance, *Linnaea* showed a positive response to fertilization in 1991, although the longer term impact of nutrient addition was strongly negative for this species. *Festuca*'s strong positive response to fertilization only lasted for 7 years and the increasingly rapid increase of *Epilobium* may now be providing competition for *Festuca* in fertilized plots.

THE EFFECTS OF HERBIVORES ALONE (TOP-DOWN CONTROL)

Two of the predictions based on the consumer control hypothesis were rejected, i.e. vegetation abundance did increase when fertilized, and species number and diversity did not decline in fenced plots unless fertilizer was also added. One hypothesis was partially accepted; *Festuca*, *Lupinus*, *Achillea*, and *Mertensia* responded to the exclusion of herbivores during the snowshoe hare peak of 148 hares km⁻² in 1990–91 (but not during the hare peak in 1998), whereas only *Achillea* and *Mertensia* increased in fertilized but unfenced plots. Otherwise there were few herbivore exclusion effects. This indicates that snowshoe hares, the major herbivore in the system, have some impact, albeit only at high densities and not during all peak years, even though hare numbers were actually slightly higher during the later peak.

There are few reported studies of the effects of exclosures in northern forested ecosystems and most of these have concentrated on the effects of larger mammals such as moose and deer on the tree and shrub layer (e.g. McInnes *et al.* 1992), although exclosures have induced significant responses in tundra vegetation (Oksanen & Moen 1994) with species capable of elevating their foliage above neighbours increasing at the expense of low-growing and prostrate species. There is little evidence however, that natural levels of mammalian herbivory limit herbaceous vegetation of the Kluane region, or affect community diversity, except during some peak years.

Herbivory nevertheless has an impact on the shrubs and trees in this region particularly during the winter

when, because of snow cover, this is the only vegetation available for browsing. Moderate browsing by snowshoe hares stimulates growth of *Salix* and *Betula*, but during peak years herbivore pressure on shrubs, especially *Betula*, is intense (Dale *et al.* 2001; Krebs *et al.* 2001b). Herbivores may have little impact on the herbaceous vegetation for a number of reasons. First, snowshoe hares may rely more on woody shrubs such as *Betula*, *Salix* or *Shepherdia* than they do on herbaceous vegetation, even in summer. Second, much of the herbaceous vegetation may be unavailable because of chemical defence (Secombe-Hett 1999). Third, we now know that snowshoe hare populations are regulated by both predators and a shortage of winter food and thus their population numbers are seldom high enough to have an impact on the herbaceous vegetation (Krebs *et al.* 1995). Although this study was not designed to discriminate between these options and each may therefore contribute to the general lack of response, the response detected during the 1990 hare peak makes regulation of hares by factors other than summer food supply the most probable explanation.

After 10 years of treatments there was a significant increase in the abundance of some of the more infrequent species (especially *Anemone* spp., *Betula glandulosa*, *Senecio lugens*, *Solidago* spp., and *Peltigera*) in the exclosed plots. This suggests that such protection may be important for the persistence of some minor components that are relatively palatable or particularly intolerant of herbivory. The actual number of rare species in the exclosed plots was however, similar to that in the control plots.

NUTRIENT AND HERBIVORE INTERACTIONS (INTERACTIVE CONTROL)

There were few interactions between exclosure and fertilization: additional growth due to fertilization was not generally removed by herbivores, vegetation abundance rarely increased inside exclosures, and plots that were both fenced and fertilized did not have the lowest species diversity.

The only species to show significant interaction effects were *Festuca*, *Linnaea*, *Epilobium* and *Achillea* from 1990 to 1992 during high hare numbers, and *Arctostaphylos* from 1994 to 1997 during the hare low. Intensity of grazing on *Festuca*, *Epilobium* and *Achillea* was greatest when the vegetation had been fertilized and the plants were then more attractive to hares. Hares therefore have a direct impact on the abundance of some species, although effects on others may be indirect. *Arctostaphylos* and *Linnaea* declined when fertilized only, but declined even more when also fenced. These prostrate species are particularly vulnerable to shading and it is quite likely that competitive effects of species such as *Festuca* or *Mertensia* may be curtailed by increased grazing on fertilized plants.

Figure 1 suggests that we might have expected more interaction effects. The vegetation composition in most

plots was fairly similar at first, but in general, plots that were fertilized (with and without fences) either increased or decreased to a greater extent than plots which were unfertilized (with and without fences). However, SEs of percentage cover are generally increasing with time (Fig. 1) and this increase may partially explain why we have few interaction effects.

TRANSIENT DYNAMICS AND LONG-TERM STUDIES

Initial responses to fertilizer and fencing treatments are species-specific, and transient (Tilman 1988). The short-term responses measured over the first few years were poor indicators of longer term changes in community composition, and perhaps the current 10 years will be a poor indicator of longer-term trends. Conclusions would have differed had the data been collected after 1 year (beginning of the hare decline), 5 years (during a hare low), or 10 years (during a hare peak) but the general trends identified may be important. It is quite likely that ecosystems such as the boreal forest understorey, where the herbaceous community is characterized by slow-growing long-lived plants, never attain equilibrium because the density of hares fluctuates, forests burn and climate changes constantly and slowly. Indeed, Nygaard & Ødegaard (1999) showed that, in the absence of any treatments, the vascular ground vegetation of a boreal forest in Norway changed markedly over a 60-year period. This means that transient response may be the only ones we have to work with, because permanent shifts in vegetation composition may not be evident until many years later, or may never be attained.

Franklin (1987) argues that another particular value of long-term studies is their potential to provide insight into rare events or episodic phenomena. In 1995 we observed the first major signs of an outbreak of spruce bark beetle. As mature trees die and the canopy becomes more open to light this will undoubtedly influence processes at ground level. *Achillea* and *Epilobium* were both minor components of the understorey vegetation of our plots until this time, but in 1996, both of these species showed dramatic increases in the fertilized plots. Both species are more typically associated with open areas and the opening of the canopy in combination with increased soil fertility probably stimulated their increase.

There are many examples of the need for longer-term observations from grasslands (Lawes *et al.* 1882; Brenchley & Warrington 1958); roadside herbaceous communities (Dunnet *et al.* 1998), and old fields (Inouye & Tilman 1995; Rajaniemi 2002). In an old field in Minnesota, changes in species composition were still occurring 10 years after the manipulations had taken place (Inouye & Tilman 1995), and in the Park Grass experiments at Rothamsted changes were still occurring after 90 years (Tilman 1988). Since many ecological processes occur slowly, initial measure-

ments are unlikely to reflect more permanent long-term responses. This will be especially critical in boreal or other high-latitude communities where the rate of response to ecological processes is slowed by low temperatures and short growing seasons; Oksanen & Moen (1994) demonstrated that responses to herbivore exclusion in tundra habitats were still occurring after 8 years. Such studies are particularly critical in systems where the species are long-lived, slow-growing, and have limited rates of dispersal and establishment.

Acknowledgements

We thank the Canadian Natural Sciences and Engineering Research Council for supporting this research programme through operating grants to RT, the Killam Foundation for a Fellowship to Elizabeth John, and the Northern Scientific Training Program for grants to many of the field assistants. We also thank Dr Andy and the Arctic Institute of North America, University of Calgary, for the use of the Kluane Lake research station; all summer assistants who have worked on this project over the years, in particular E. Klein and J. McDowell. RT expresses his appreciation to Kâni Işık and Kayahan Fişkin, Akdeniz University Biology Department, Turkey, for providing a quiet place to write while on sabbatical, and TÜBİTAK (Turkish Scientific and Technical Research Institute) for providing research support while in Turkey. We also thank four anonymous referees whose input considerably improved this paper. This is publication no. 172 of the Kluane Boreal Forest Ecosystem Project.

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