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Herbs and Grasses

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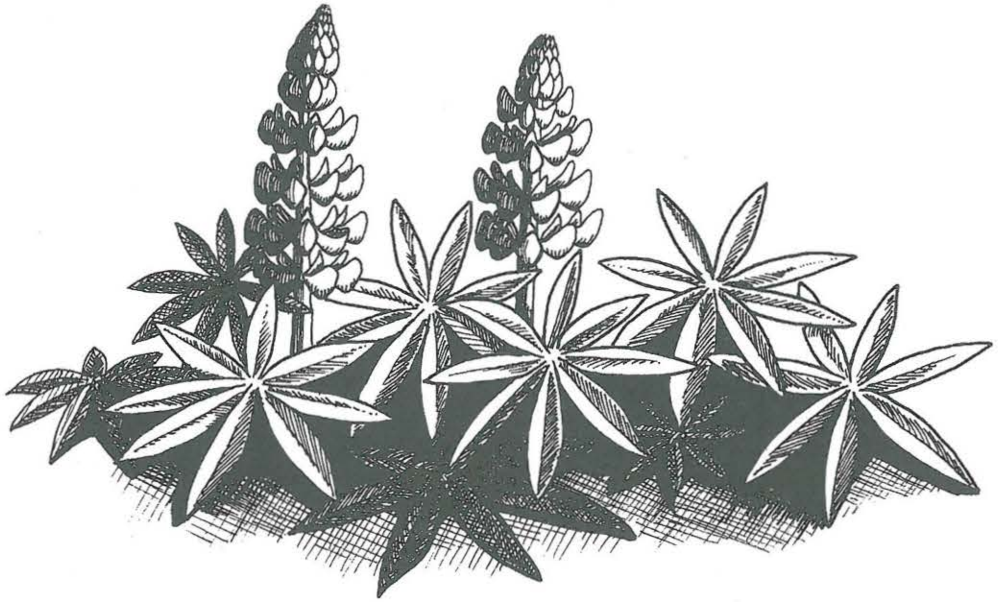


Plants in the boreal forest are an important component of the ecosystem for two main reasons. First, the plants as vegetation form the physical surroundings for both herbivores and carnivores and are the basis of the physical structure of the community. Second, as primary producers, they provide the energy and nutrients to the herbivores on which higher trophic levels depend. Therefore, understanding the factors that limit the quantity and the quality of plants is fundamental. Our studies focus on the herbaceous vegetation but primarily on two grasses, *Festuca altaica* and *Calamagrostis lapponica,* which dominate small meadows scattered throughout the white spruce forest, and on the four herbs, *Lupinus arcticus, Anemone parviflora, Mertensia paniculata,* and *Achillea millefolium* var. *borealis,* which are relatively abundant in the forest understory (see the appendix following this chapter). These plants provide a source of high-quality food to the herbivores.

Soil nutrients, especially nitrogen, often limit the productivity of boreal forest vegetation (Bonan and Shugart 1989) and may control vegetation standing crop. Plants differ in their abilities to respond to increased nutrient levels, and community composition usually changes after fertilization as more competitive species begin to dominate. The nutrient availability level also influences a species' ability to produce defensive chemical compounds against herbivory (Coley et al. 1985) and the ability to regrow after herbivory (Hilbert et al. 1981, Maschinski and Whitham 1989). Conversely, herbivory may have a direct effect on vegetation quantity and quality. Herbivory has long been known to influence species composition in some plant communities (Huntly 1991) due to differential plant palatability and differences in plants' abilities to tolerate herbivory. Many plants produce defensive chemical compounds in response to herbivory (Palo and Robbins 1991, Tallamy and Raupp 1991). The snowshoe hare has distinct preferences among the summer forage species available in the boreal forest (Bryant et al. 1991).

5.1 Hypotheses Regarding Vegetation

For the purposes of the Kluane study, we considered the soil to be a trophic level. The herbaceous vegetation, along with the soil nutrient pool, forms two of the four trophic levels recognized in this system. To understand some of the inter-trophic linkages between components of the system, three hypotheses regarding the vegetation were tested: that vegetation was controlled by (1) nutrient availability alone (bottom-up, or donor control), (2) herbivores alone (top-down control), and (3) both nutrient availability and herbivores. This involved three major experimental treatments: fertilization, herbivore exclusion, and fertilization plus herbivore exclusion. These treatments allowed us to make specific predictions about changes in plant biomass, or standing crop, under the three different hypotheses (table 5.1). In some cases, however, response was also assessed using changes in rates of plant turnover, plant nutrient content, or secondary compounds. In addition to the direct predictions in table 5.1, some subsequent predictions were also made; these predictions are formalized below.

Hypothesis 1: Vegetation is controlled by nutrient availability alone.
This bottom-up, donor control, hypothesis makes five predictions:

1. With fertilization there will be an overall increase in the total biomass or standing crop of herbaceous vegetation.
2. Alternatively, there will a greater nutrient content of vegetation in fertilized areas.
3. There will be no increase in vegetation standing crop when herbivores are excluded.
4. Vegetation composition will change as more competitive species replace stress tolerators in fertilized areas.
5. If vegetation is removed from a plot, there will be an increase in soil nutrient levels.

Hypothesis 2: Vegetation is controlled by herbivores alone.
This top-down hypothesis makes two predictions:

1. There will be no increase in vegetation standing crop with fertilizer, especially during the snowshoe hare peak.
2. Assuming snowshoe hares are the major herbivore, then in hare exclosures, vegetation standing crop will increase and secondary compound content will decrease.

Hypothesis 3: Vegetation is controlled by both nutrient availability and herbivory.
This interactive hypothesis makes four predictions:

1. There will be an increase in plant productivity in fertilizer plots, but biomass will remain unchanged.
2. On fertilizer plots, grazing intensity will increase due to increased quality of forage.
3. In hare exclosures, vegetation standing crop will increase and secondary compound content will decrease.
4. In hare exclosures, soil nutrient levels will be lower than in control plots immediately outside of the exclosures because the larger, protected and ungrazed plants will extract more nutrients from the soil.

Table 5.1 Predictions of the direction of change in plant biomass, or standing crop, from each of the three experimental treatments according to the three models of community organization.

Model	Fertilizer Added	Herbivores Excluded	Fertilizer Added, Herbivores Excluded
Bottom-up, donor control	+	0	+
Top-down, herbivore control	0	+	+
Interactive control	+	+	+

+ = biomass increase, 0 = no change.

5.2 Study Area

The vegetation in our area is dominated by white spruce (*Picea glauca*), with a shrub understory dominated by gray willow (*Salix glauca*) and dwarf birches (*Betula nana* and *B. glandulosa*). The herb layer (including dwarf shrubs) includes *Lupinus arcticus, Festuca altaica, Calamagrostis lapponica, Mertensia paniculata, Anemone parviflora, Achillea millefolium* var. *borealis, Linnaea borealis, Arctostaphylos uva-ursi, Epilobium angustifolium,* and *Solidago multiradiata* (CD-ROM frame 44). Some of the studies used the already established grids, especially the two 4-ha hare exclosure grids described in chapter 4; one of these was fertilized. Most of the other studies described were done at two sites in areas of moderately open white spruce forest with a well-developed herbaceous understory. The first site was at Boutillier summit (km 1690.4, Alaska Highway), about 50 m into the forest to the north of the highway, and the second site was about 3 km to the south near a Microwave tower.

5.3 Tests of Predictions from Three Models

The experimental treatments for most of the Kluane study were either the 4-ha herbivore exclusion grids or the larger grids of approximately 1 km^2. However, most of the herbaceous work was done at a smaller scale either as a subsample within a major grid (e.g., predictions 1.1, 1.3, 2.2, 3.3, 3.4), or on 5 m × 5 m or smaller plots. We adopted this approach to minimize the strong heterogeneity that was so visually apparent in the distribution and abundance of the herbaceous vegetation; to have included this heterogeneity by using larger sampling areas would have undoubtedly obscured real patterns that occur within the herbaceous vegetation. We typically chose sites that had most of the major herbaceous species present and in which each of the study species were typically at least 10% of the vegetation cover. This reduced effects introduced by sites that had unusual species composition or had a lot of bare ground.

5.3.1 Donor Control Model

The five predictions that we tested from the overall model that vegetation is controlled by nutrient availability had a variety of results.

Prediction 1.1: Fertilization Will Result in an Overall Increase in the Amount of Herbaceous Vegetation This prediction was verified for most species, but rejected for *Anemone* and *Lupinus.*

The density and biomass of selected species were estimated on both of the fertilized grids and immediately adjacent to the grids. Sampling was done in both closed spruce and open spruce forest at all sites. Fertilization began in 1987 but detailed sampling did not begin until 1993 (Turkington et al. 1998). Sampling was done during July when herb biomass is at a peak. The probability of *Mertensia* being present and the number of flowering stems on each *Mertensia* increased when plots were fertilized (figure 5.1). For the other species, *Achillea millefolium* and *Solidago,* fertilization had little effect. The dry mass of most species, whether flowering or nonflowering (figure 5.1), increased in closed sites when fertilized. Only *Epilobium* increased (nonflowering) in an open site. In addition fertilizer had a significant effect on the growth of *Festuca altaica* and *Calamagrostis lapponica* after only one season (D. Hik, unpublished data).

Arii (1996) investigated the effects of fertilization on *Achillea, Anemone, Festuca, Lupinus,* and *Mertensia. Achillea* and *Festuca* increased biomass and leaf number with fertilization, but *Mertensia* and *Lupinus* remained unchanged (figures 5.2, 5.3). At the highest level of fertilization, there was high mortality (almost 80%) in the *Anemone* population (figure 5.3). The individualistic response of these species means that prediction 1.1 cannot be applied to all herbaceous species.

Prediction 1.2: Vegetation in Fertilized Areas Will Have Greater Nutrient Content but No Increase in Standing Crop This prediction was verified for *Anemone, Epilobium, Lupinus, Mertensia,* and *Achillea.*

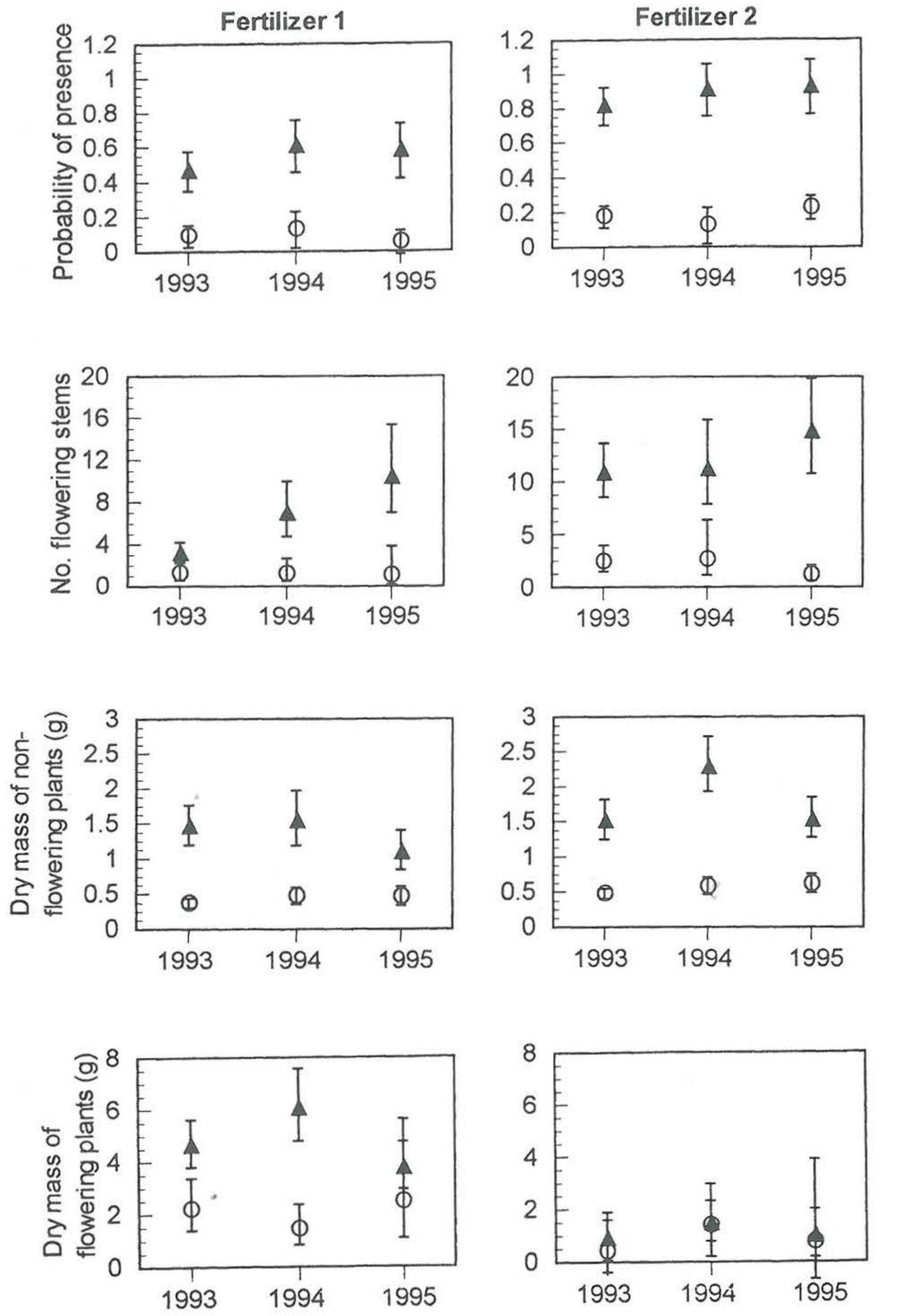


Figure 5.1 The abundance and growth of *Mertensia paniculata* in closed white spruce forest on the fertilizer 1 and fertilizer 2 grids (▲) and adjacent to the grids in unfertilized (○) plots. Error bars are 95% confidence limits.

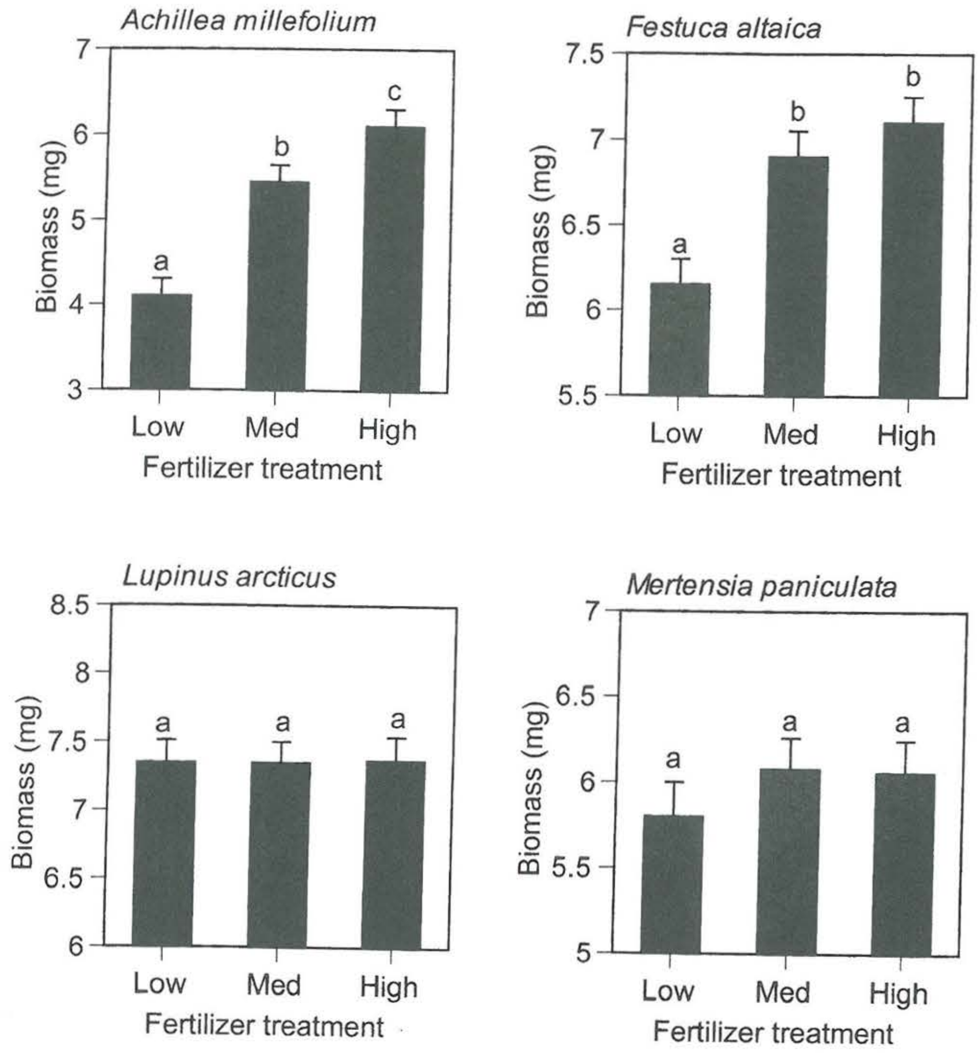


Figure 5.2 Average dry mass (± SE) (log transformed) of four species at final harvest in 1994, growing at three levels of fertilization (low = not fertilized; medium = 200 g/m^2; and high = 400 g/m^2 of water-soluble 6:8:6 NPK). Within a panel, bars that share a common letter are not significantly different ($p > .05$; least significant difference).

We analyzed the effect of fertilizer treatment on the levels of available nitrogen and free amino acids in *Anemone, Epilobium, Lupinus, Mertensia,* and *Achillea* during the 1991 growing season. Fertilized and unfertilized plants were sampled at three dates through the growing season, and on each date, young, old, and medium-aged leaves were removed for analysis. Fertilized plants of all species had increased nitrogen content. The percentage of nitrogen decreased as the season progressed in both control and treatment plots. The amino acids serine, asparagine, γ-aminobutyric acid, cystine, arginine, and valine all showed substantial increases after fertilization; other amino acids did not increase relative to controls. Asparagine and arginine, which are used to transport and store nitrogen, were the two most abundant amino acids in these plants and, with fertilizer addition, increased more (8.5× versus a maximum of 3×) than the other amino acids. Changes in the levels of specific amino acids depended on the species and on the date of sampling.

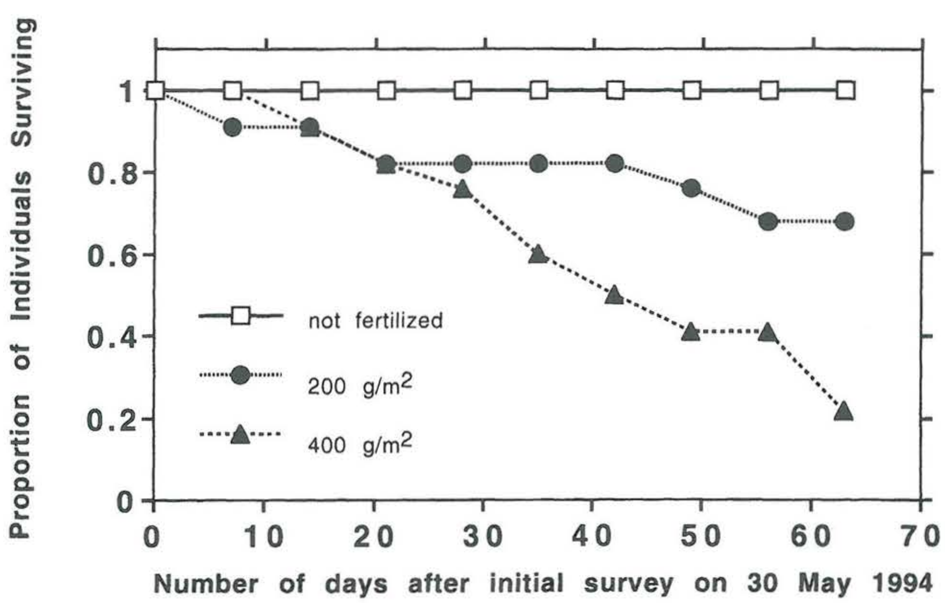


Figure 5.3 Differential survival of three natural populations of *Anemone parviflora* ($n = 12$ for each population) in 1994, growing at three levels of fertilization. Fertilizer was added as a solution of 6:8:6 NPK.

Prediction 1.3: Standing Crop Will Not Increase When Herbivores Are Excluded Extensive vegetation sampling of both hare exclosure grids was conducted in the summers of 1991–1995, typically in late June. At each site we established eight 40-m transects, each of which was bisected by the exclosure fence. Leaf area index was estimated in 1 m × 50 cm quadrats placed at 4-m intervals along each transect. No consistent significant differences were found between the herbaceous vegetation inside and outside of the fences since 1992, when a number of species showed weak responses to the fences; these surveys were done immediately after a peak in snowshoe hare densities.

Prediction 1.4: Vegetation Composition Will Change as More Competitive Species Replace Stress Tolerators Sixteen 5 m × 5 m plots were chosen at both the Boutillier and Microwave sites for a 2 × 2 factorial experiment (with and without fertilizer, with and without grazing enclosures) (John and Turkington 1995, Turkington et al. 1998). We applied a high nitrogen fertilizer once per year from 1990 to 1995, at the same rate as on the main treatment grids. This was done just after snow melt, early in the growing season in late May and early June. Twice each summer a survey of the percent cover of all plants less than 1 m tall was made in each plot. To minimize trampling effects, each plot was divided into five untrodden experimental and sampling zones, 5 m long, with 15-cm wide

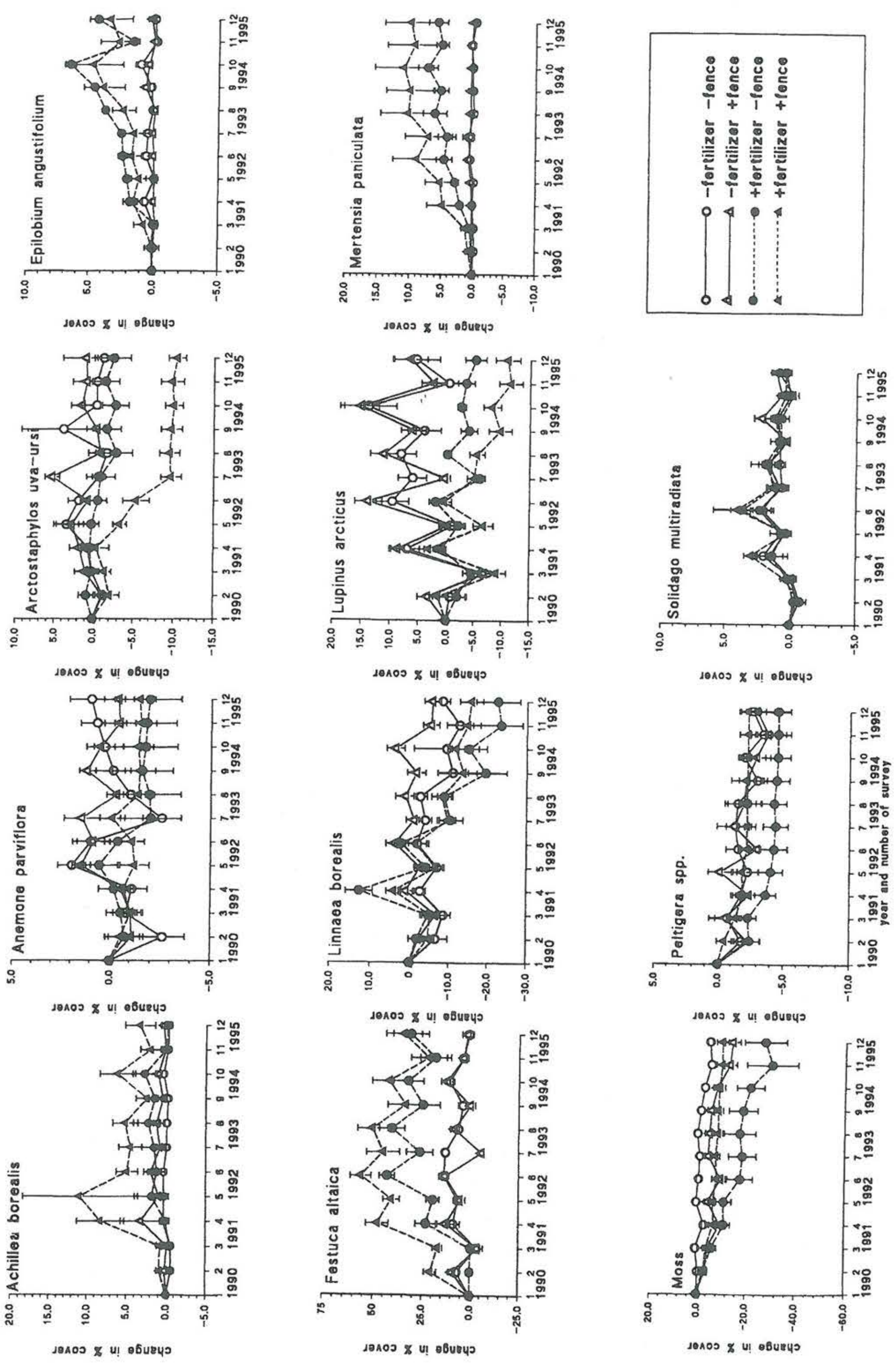


Figure 5.4 Change in percent cover (mean ± SE) for 11 herbaceous and dwarf shrub species in a 2 × 2 factorial experiment in plots at the Microwave and Boutillier Summit sites from 1990 to 1995. Treatments (fertilizer and fences) were first imposed in May 1990, and fertilizer was added each year in late May.

walkways between each zone. Fences were 1 m high and made of galvanized chicken wire with 2.5-cm mesh, supported by 2-m high T-bars, and were firmly stapled to the ground to prevent animals from getting under the fence. Unfenced plots also had T-bars with string between them to prevent casual trampling by data collectors. No fence damage was recorded, and there was no evidence that large mammals, such as moose, entered the exclosures during the winter.

We investigated the effects of exclosure, fertilizer addition, and time for 11 of the most frequently occurring species. The eleven species analyzed showed a range of responses to the treatments (figure 5.4; CD-ROM frame 45). Ten showed a significant fertilizer effect, with four increasing in response to fertilizer (*Mertensia, Festuca, Achillea,* and *Epilobium*) and six decreasing over the 6-year period (*Anemone,* various species of moss, *Peltigera, Linnaea, Arctostaphylos,* and *Lupinus*). Not all fertilizer effects were immediately apparent, with some species showing an initial positive or neutral response to fertilizer, which later reversed (e.g., *Linnaea*). Fertilization altered the species composition of small meadows in favor of *Calamagrostis* over *Festuca* (D. Hik, unpublished data). Fertilizer effects on herbs in the boreal forest are highly individualistic and do not follow a single prediction like hypothesis 1. However, in general, it is evident that long-term fertilization causes a shift from a herb-dominated community to one dominated by grasses.

In general, the untreated (control) community is rather static from year to year (figure 5.4). But even in the control plots, some species such as *Anemone* and *Lupinus* fluctuate from year to year. *Achillea* and *Arctostaphylos* responded fairly quickly to fertilizer addition, but this effect diminished with time, and no significant differences were detectable in surveys 11 and 12 in 1995. The response of *Linnaea* to fertilizer did not become apparent until later surveys.

Prediction 1.5: If Vegetation Is Removed from a Plot, Soil Nutrient Levels Will Increase In these northern spruce forests, soils develop in a cool and moderately humid climate. The decomposition of plant remains is slow, and the surface of the soil is covered by a mat (mostly spruce needles) of partly decomposed, acidic, plant material, which is quite sharply separated from the underlying soil. Beneath this mor litter layer, the upper soil is leached and typically grayish. The leached layer is acidic and low in nitrates and most other plant nutrients. In 1996 P. Seccombe-Hett (unpublished data) identified three hundred 1-m^2 plots beside the hare exclosure grid. In 150 of them vegetation was killed by applying Roundup (Monsanto Corp.); the other 150 were left untreated. Soils were sampled for nitrate nitrogen in early July, 4 weeks after vegetation removal. Nitrate nitrogen levels were significantly higher ($p < .1$) in those plots in which the vegetation had been removed.

5.3.2 Herbivore Control Model

We tested two predictions that follow from the idea that vegetation is controlled solely in a top-down manner by the amount of herbivory.

Prediction 2.1: Fertilizer Will Not Increase Vegetation Standing Crop This prediction has largely been rejected in our previous discussion of prediction 1.1. However, after six growing seasons (using the same 5 m × 5 m plots as in prediction 1.4), four species, *Achillea, Festuca, Arctostaphylos,* and mosses, responded significantly to the exclusion of herbivores (figure 5.4). Responses varied, but notably, *Achillea, Festuca,* and *Mertensia* increased when fertilized, but they had an even greater increase when fenced as well. This indicates that some portion of the additional productivity due to fertilization was being consumed in the unfenced plots. Therefore, although hares affect the standing crop of these three species, they do not affect the standing crop for the other five species monitored. These data are more consistent with prediction 3.1. In general, where herbivore density is at natural levels, the impact of herbivores on vegetation biomass is slight; however, even fairly moderate applications of fertilizer will induce noticeable changes in vegetation. Fertilizing causes a major decline in moss in those plots not protected from grazers and a decline in *Arctostaphylos* in those plots protected from grazers (figure 5.4). *Lupinus* (a legume), *Linnaea,* and *Arctostaphylos* decrease, while *Mertensia* and *Festuca* increase, when fertilized and fenced. One species, *Solidago multiradiata,* was remarkable in its lack of response to treatments, showing no tendency at all to respond to the experimental manipulations even after 6 years.

Prediction 2.2: Vegetation Standing Crop Will Increase in Hare Exclosures Tests of prediction 1.3 demonstrated that there were no changes in vegetation biomass or species composition inside the hare exclosures. An additional study in the summer of 1991 (John and Turkington 1995) was conducted using four paired plots at each of five of the hare trapping grids that provided a range of snowshoe hare densities. Each pair consisted of a fenced and adjacent unfenced plot, each 1 m × 1 m. After 8 weeks, above-ground biomass was harvested from all plots and sorted to species. At all sites, there was less *Festuca* and *Achillea* in the unfenced plots, and at four of the five sites there was less total biomass outside than inside. Analyses revealed that even though there were apparently some effects by herbivores these responses occurred only when snowshoe hare densities were artificially high.

5.3.3 Combined Top-down Bottom-up Model

Many community studies suggest that neither the top-down nor the bottom-up model of community organization is adequate and that one needs to consider a combination of these two models (see chapter 3). Here we were able to test four predictions that flow from a combined model.

Prediction 3.1: Plant Productivity Will Increase in Fertilizer Plots but Biomass Will Remain Unchanged This prediction was verified for *Mertensia* but rejected for *Anemone* and *Lupinus.*

We must discriminate between *plant standing crop* or *biomass* (i.e., how much vegetation present at any particular time [see prediction 1.1]), and *plant productivity* (i.e., how much is produced). The productivity of a system can be increased by fertilization, but the standing crop remains unchanged if the additional productivity is consumed by herbivores. Addressing this prediction required detailed and frequent monitoring of populations of individual species. Two studies were done. The first used the 5 m × 5 m grids described earlier (prediction 1.3). Within each of the thirty-two 5 m × 5 m plots, we selected three populations each of *Anemone* and *Mertensia.* These are common herbaceous species in the forest understory and are eaten by snowshoe hares. The location of each population was permanently marked, and all plants were individually labeled. Initially we began monitoring 700 *Anemone* and 854 *Mertensia.* Populations were surveyed three times per season. For each stem we recorded the number and size of leaves and the number of leaf buds and flowers. The total leaf length per stem was calculated from the sum of the leaf lengths (John and Turkington, 1997).

Both species responded more strongly to fertilizer addition than to the exclusion of herbivores. *Mertensia* produced more stems, more flowering stems (figure 5.5a), more leaves per stem (figure 5.5b), and increased total leaf length per stem (figure 5.5c) for nonflowering stems in the fertilized plots. Analysis of variance detected a significant fertilizer and exclosure effect in most years of the study. *Anemone* showed contrasting responses at the individual and population levels; although individual stems produced slightly (and significantly) more leaves in fertilized plots (figure 5.5e), the population density declined (figure 5.5d). There were no strong effects on either leaf size or flowering. There is evidence of higher leaf turnover in fertilized plants (a proportionally higher production of buds, more rapid decline in leaf number at the end of the growing season, and greater fluctuation in leaf number throughout the season), but there must ultimately be a higher death than birth rate, both at the leaf and the stem level, leading to the observed population decline.

In a second study, Graham (1994) and Graham and Turkington (2000) investigated the effects of various treatments on the population dynamics of *Lupinus* using a 2 × 2 × 2 factorial cross of ± fertilizer, ± simulated herbivory, and ± neighbor removal applied to 1-m^2 quadrats. These quadrats were fenced to exclude hares and other large mammalian herbivores. They were surveyed every second week during the 1991 and 1992 growing seasons, and 11 different demographic and growth variables were measured. The *Lupinus* populations were remarkably unresponsive to treatments, even by the end of the second season (figure 5.6; CD-ROM frame 45). In addition, Graham tagged 320 clumps of *Lupinus* and at regular intervals recorded the condition of the leaves. This measure was used to calculate an index (live summer leaf-days) of plant availability to herbivores by counting the mean number of leaves that are available as food and how many days those leaves had been alive and available for consumption (Graham 1994, Graham and Turkington 2000). By the end of the second growing season the only significant effect was a decrease due to fertilization, where the mean live summer leaf-days for the fertilized treatment was 14070 and in controls 25561 (figure 5.7).

Prediction 3.2: Grazing Intensity Will Increase on Fertilized Plots Due to Increased Quality of Forage To assess this prediction requires a careful examination of figure 5.4. If grazing intensity increases in fertilized plots, then two conditions must be met. First, the amount of change between the treatments no fertilizer, no fence and no fertilizer, with fence should be less than the difference between fertilizer added, no fence and fertilizer added, with fence. This describes a situation where the addition of fertilizer alone, without herbivores, will change the vegetation biomass (either an increase or decrease), but the change will be moderated in fertilized plots that have the herbivores present because they remove some of the presumed higher quality vegetation produced. The degree of moderation will be greatest where the intensity of grazing is greatest. Second, the percent cover of species in fertilized plots must be higher in those plots that are fenced compared

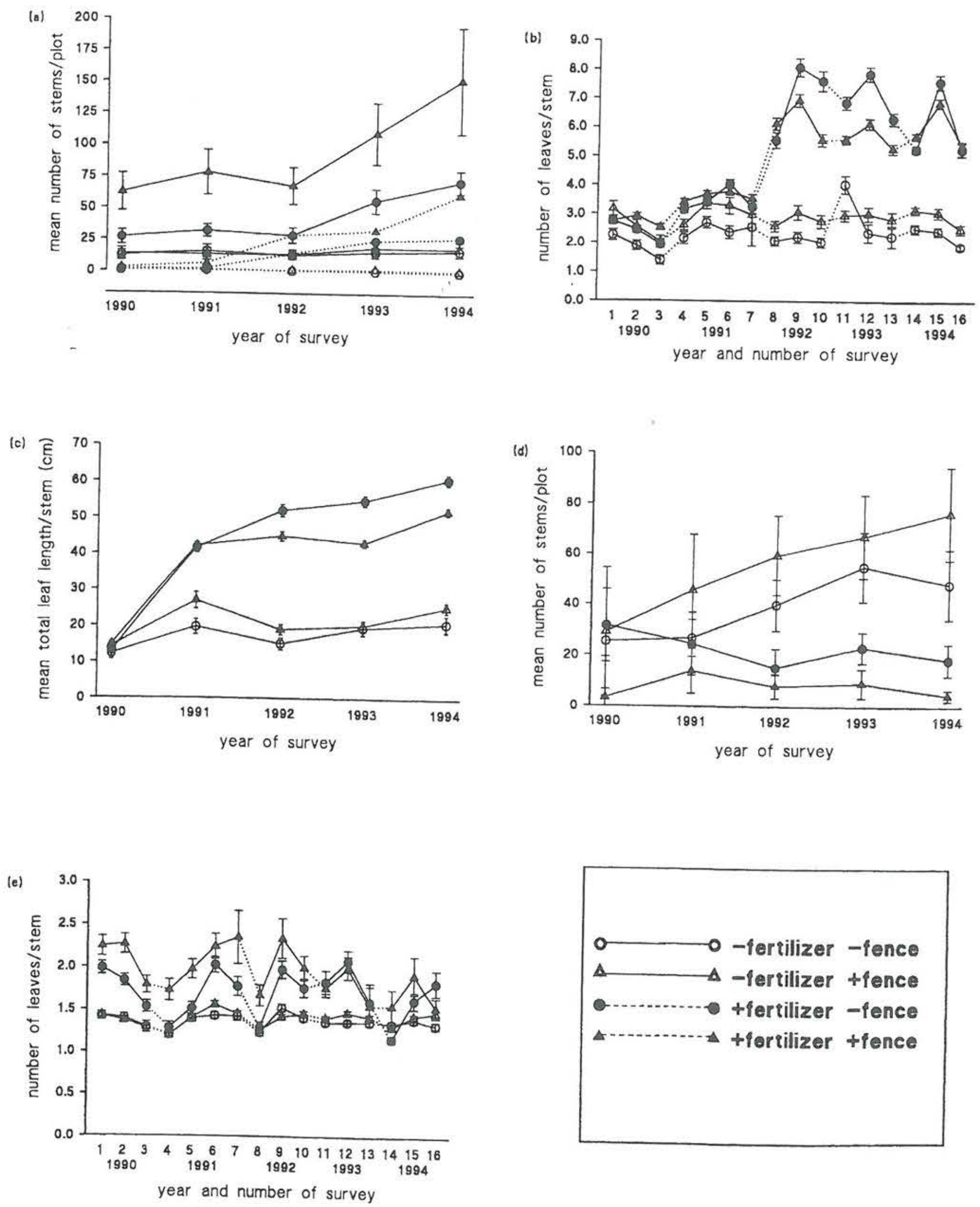


Figure 5.5 The effects of fertilization and small mammal exclosures on the growth of *Mertensia* (a–c) and *Anemone* (d, e). (a) Mean (± SE) number of stems per plot, by treatment in the mid-season survey. The contribution of flowering plants to the total is shown by the dotted lines. (b) Mean (± SE) number of leaves per stem for the whole population through all surveys. Solid lines join data from the same year, dotted lines connect data from different years. (c) Mean (± SE) total leaf length per stem (cm) for the mid-season surveys of each year. (d) Changes in mean number of stems per plot, expressed as a proportion of the original number of stems in each treatment. (e) Mean (± SE) number of leaves per stem. Solid lines join data from the same year; dotted lines connect data from different years.

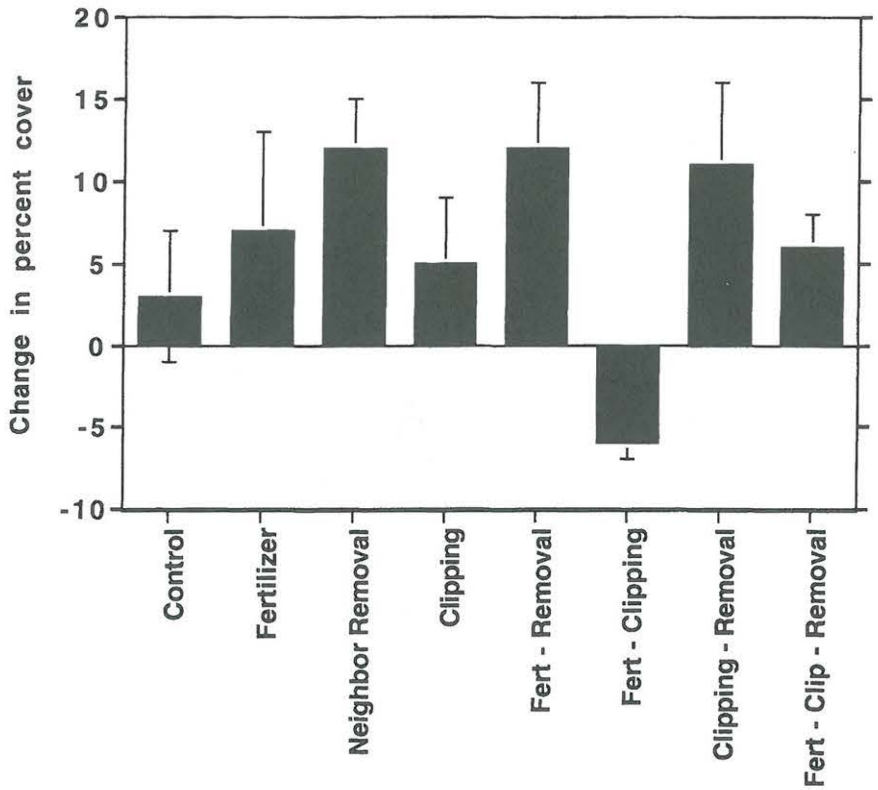


Figure 5.6 Mean (± SE) change in percent cover of *Lupinus arcticus* in response to fertilization, clipping, and removal of neighbors, from June 1991 to August 1992.

to unfenced plots (i.e., fertilized, no fence should have lower percent cover values than fertilized, fenced). In figure 5.4, five species meet these criteria—mosses, *Festuca, Achillea, Mertensia,* and *Peltigera*—and the prediction can be accepted for these species.

In a second study, Dlott (1996) did a transplant experiment to investigate the combined effects of fertilizer and herbivory on plant growth (CD-ROM frame 45). Eight species were transplanted into an experimental design of ± herbivory (fences) crossed with no added nitrogen, 12 g N/m^2 or 35 g N/m^2, on each of three grids (fertilizer 1, food 1, and predator exclosure + food) representing different densities of grazing animals. Survival (figure 5.8), number of leaves (figure 5.9), and plant height were surveyed weekly in 1992 and monthly in 1993. Percent cover surveys were taken in 1993 to investigate treatment effects on existing vegetation. Results indicate that there is no top-down effect at natural nutrient levels, and differences inside and outside exclosures were only significant when grazing pressure and nutrients were experimentally high (CD-ROM frame 45). This result is consistent with short-term exclosure experiments described in John and Turkington (1995).

The effects of fertilizer addition and clipping intensity on the potential of plants to regrow after grazing were examined (Hicks and Turkington 2000). Individuals of *Festuca, Achillea,* and *Mertensia* were transplanted to plots and subjected to three levels of clip-

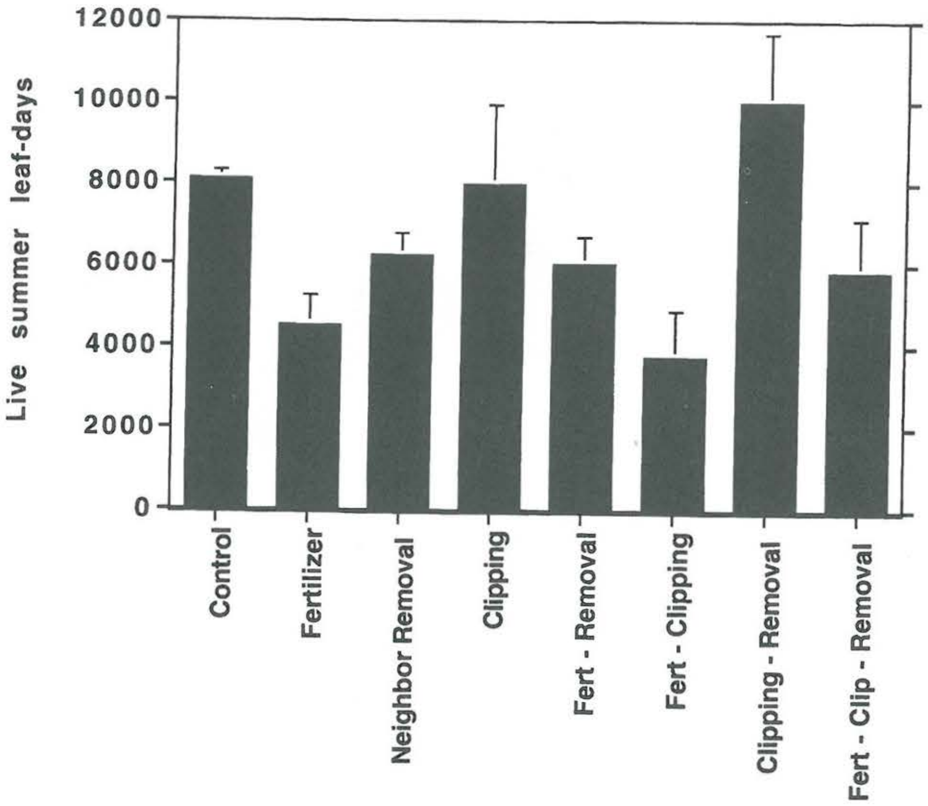


Figure 5.7 The effects of fertilization, clipping, and removal of neighbors on the availability of leaves of *Lupinus arcticus*, measured as live summer leaf-days (± SE), to herbivores. This index is the number of days each leaf is alive during the summer of 1992 summed over all leaves.

ping (none, 50% leaf loss, and 100% leaf loss) and two levels of fertilizing (none and 15 g N/m^2). Plant growth was assessed using biweekly measurements of total leaf area per plant, and individuals were harvested at the end of the growing season to obtain final biomass estimates. After 100% leaf loss, unfertilized *Festuca* grew as much new leaf area as the unclipped plants and ended up approximately half the size of the unclipped plants (figure 5.10). Unfertilized *Mertensia* regrowth was significantly increased when clipped because it could fully compensate for tissue loss by the end of one growing season. When fertilizer was added, clipped individuals of each species regrew significantly less than the unclipped controls

Prediction 3.3: Vegetation Standing Crop in Hare Exclosures Will Increase and Secondary Compound Content Will Decrease This prediction is the same as prediction 2.2, discussed above.

Prediction 3.4: Soil Nutrient Levels in Hare Exclosures Will Be Lower Than in Control Plots Immediately Outside of the Exclosures This prediction was tested by

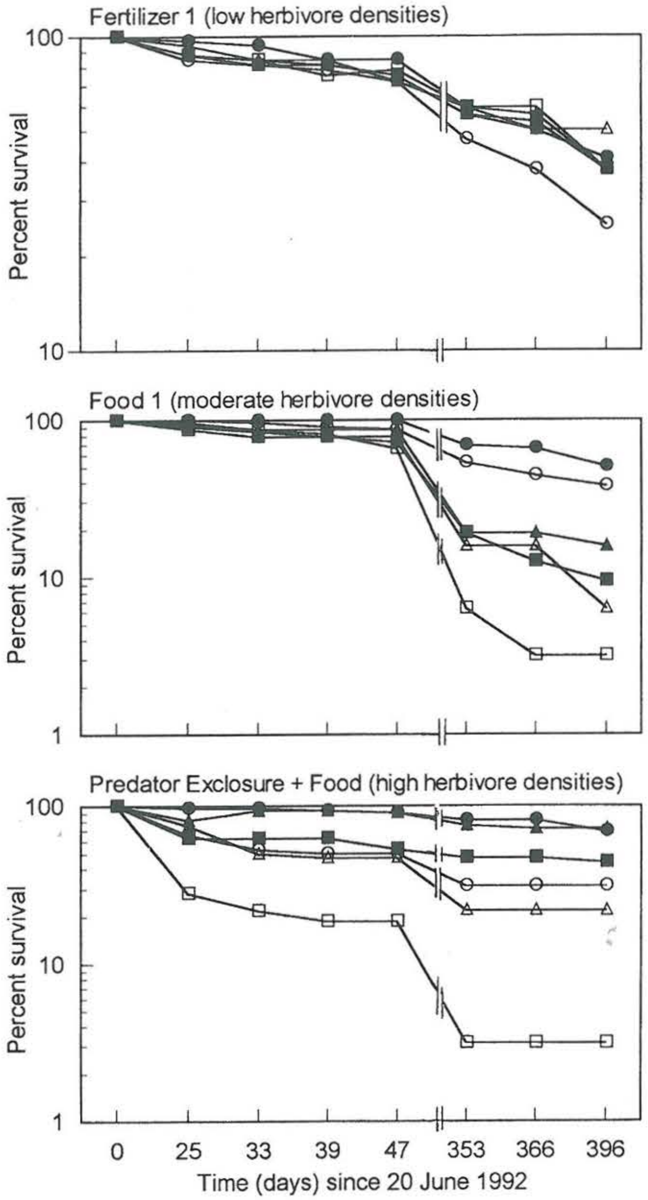


Figure 5.8 Differential survival of transplanted seedlings at the fertilizer 1 (lowest hare density), food 1, and predator exclosure + food (highest hare density) grids. On each grid, plots were either fenced (filled symbols) or unfenced (open symbols) and treated with one of three levels of fertilizer application: none (○,●), 11.6 g N/m^2 (△,▲), and 35 g N/m^2 (□,■).

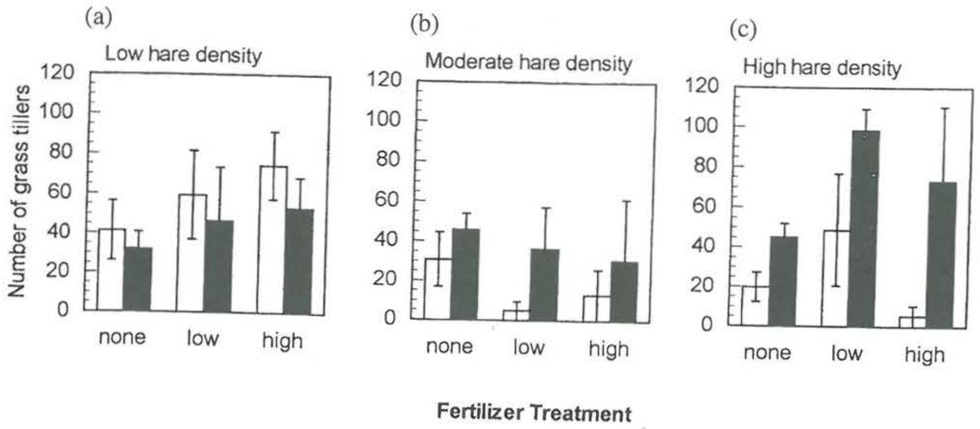


Figure 5.9 Number (± SE) of grass tillers in plots on three grids providing different densities of snowshoe hares in July 1993. (a) Fertilizer 1 (lowest hare density), (b) food 1 (moderate hare density), and (c) predator exclosure + food (highest hare density). Solid bars represent fenced plots; open bars represent no fence. Low fertilizer is 11.6 g N/m^2 and high is 35 g N/m^2.

Seccombe-Hett (see prediction 1.5). She showed that soil nitrate nitrogen levels were higher ($p < .05$) inside the hare exclosure than outside.

5.4 Which Model Best Describes Boreal Forest Herbs and Grasses?

The majority of the data presented supports the hypothesis that herbaceous vegetation standing crop is controlled by nutrient availability alone, the bottom-up model of community organization (table 5.2; Turkington et al. 1998). With fertilization there was an overall increase, up to threefold after 3 years, in the amount of herbaceous vegetation, especially among the grasses *Festuca* and *Calamagrostis*. In addition, there was a greater nutrient content of vegetation in fertilized areas. The one study designed specifically to investigate the rate of turnover of standing crop in response to fertilization did not support the hypothesis of higher turnover. This study used *Lupinus,* which, in hindsight, was an inappropriate choice of test species. Of the many common species in the area, a few (e.g. mosses, *Peltigera, Linnaea,* and *Arctostaphylos*) had variable responses to the addition of fertilizer, but only *Anemone* and *Lupinus* consistently failed to increase in abundance when fertilized. It was initially unexpected that soils inside the herbivore exclosure should have more nitrate nitrogen than soils in off-grid plots. However, results from some of the other studies showed that when vegetation is grazed, some of the species increase their relative growth rates. This additional growth due to grazing outside the exclosures may reduce nutrient levels to below those in the ungrazed exclosures.

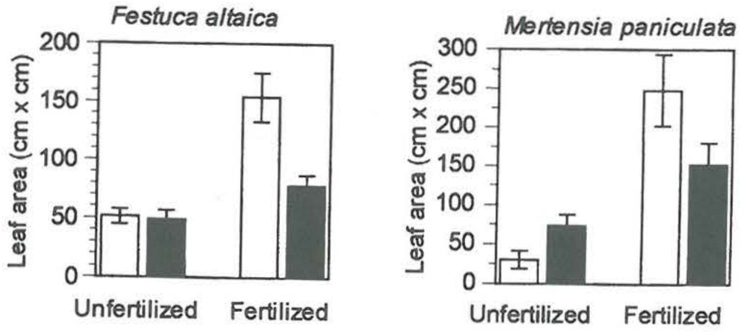


Figure 5.10 Leaf area (± SE) regrowth (cm^2) of *Festuca altaica* and *Mertensia paniculata* after a clipping (filled bars) treatment on fertilized and unfertilized plots in 1995, compared with new growth on unclipped (clear bars) plants.

Table 5.2 Predicted, and overall direction of change in plant biomass (or nutrient content), or standing crop, from each of the three experimental treatments according to the three hypotheses.

	Fertilizer Added		*Herbivores Excluded*		*Fertilizer Added, Herbivores Excluded*	
Model	Predicted	Observed	Predicted	Observed	Predicted	Observed
Bottom-up, donor control	+	Mostly verified (1.1, 1.2)	0	Verified (1.3)	+	Rejected (1.3)
Top-down control	0	Mostly rejected (2.1)	+	Rejected (2.2, 3.3)	+	Rejected (1.3)
Interactive control	+	Some support (3.1, 3.2)	+	Rejected (2.2, 3.3)	+	Rejected (1.3)

Numbers in parentheses refer to predictions in text. + = biomass increase, 0 = no change. There was variability in species' response to treatments in most cases; this table summarizes the overall direction of change.

The remainder of the studies indicate that the impact of mammalian herbivory, primarily by hares, on the boreal forest understory abundance and composition is minimal compared to that of fertilizer addition. Only *Achillea, Festuca, Arctostaphylos,* and mosses responded significantly to the exclusion of herbivores. We have been able to show some herbivory effects, but only when herbivore numbers were artificially elevated or when the vegetation was fertilized and the plant was significantly more attractive to hares. Herbivory effects are evident in the 5 m × 5 m plots where the results clearly show that the intensity of grazing increases when plots are fertilized. In addition, Dlott's (1996) study demonstrated herbivory effects, but only when herbivore numbers were experimentally elevated to artificially high levels.

Overall there is little evidence that natural levels of mammalian herbivory limit herbaceous vegetation of the Kluane region or affect its composition. In this area, herbivory has a major impact on the woody vegetation (see chapter 6), so the lack of response seen in the herbaceous vegetation could be due to a number of factors: (1) although snowshoe hares eat herbaceous vegetation, they do not eat enough to have an effect on plant population processes, relying on the woody vegetation for the bulk of their diet, even in summer. (2) If hare populations are more limited by a shortage of winter than summer food, then their populations may be maintained at a level below that at which an effect on the summer vegetation is seen. (3) Although apparently available, a large portion of the herbaceous vegetation may well be unavailable due to chemical defense. (4) These experiments were set up during a period of high snowshoe hare densities (1990) and in the 2 subsequent years the density of hares declined dramatically. It is quite possible that in the decline phase of the snowshoe hare cycle the hare's impact on its food supply is less than at other times. Ideally, this work would have begun 2–3 years earlier when snowshoe hare densities were increasing. This would have allowed us to assess the impact of herbivory during the 3 or 4 years of highest herbivore densities rather than the 2 years we were able to monitor.

Another of the primary predictions made was that, in response to fertilization, vegetation composition would change as more competitive species replace stress tolerators. Boreal plant communities are generally nutrient limited, particularly by nitrogen (Chapin and Shaver 1985, Bonan and Shugart 1989). When fertilizer is added to such low-nutrient communities, it will differentially promote the growth of some species, leading to changing light and moisture conditions for their neighbors. The effects range from causing a dramatic increase in abundance to causing a decline. These differential changes in biomass will in turn affect competitive relationships and lead to shifts in relative abundance and species diversity. *Achillea, Festuca,* and *Mertensia* increased in percent cover when fertilized, while *Anemone* declined. *Festuca* shows the most dramatic increases in abundance, from 20% to greater than 50% cover in fertilized plots. It is likely that the declines after fertilizer addition for some species are due to competition from the more rapidly growing species, especially *Festuca.* However, Arii's (1996) study demonstrated that *Anemone* suffered increased mortality with increasing levels of fertilizer, with or without neighbors, so mortality can be due to competition or due to the direct effects of fertilizer alone. In general, these results support current theory about the nature and process of plant competition for nutrient resources (Grime 1977, Tilman 1988), in which, as the ratio or total abundance of resources changes, species composition also changes. The results reported here are largely consistent with those of Nams et al. (1993), which showed an increase in *Festuca, Achillea,* and *Epilobium* with fertilization.

Increased nutrient uptake may be diverted into structures other than vegetative biomass. For example, reproduction may increase with nutrient levels. The total number of flowering stems of *Mertensia* increased only after 2 years, suggesting that there is a time lag between the acquisition of resources and the production of flowering stems. A high investment in flowering may divert resources from vegetative structures. However, as flowering stems in *Mertensia* are taller and have more leaves than nonflowering stems, their production may be an advantage in competing in a more productive community. *Mertensia* seedlings were not observed within our study plots, despite the large number of flowers produced. In recent long-term experiments on graminoids, Shaver and Chapin (1995) similarly found an increased production of ramets after 1 year of fertilization, followed by increased flowering in the second year.

5.4.1 *Transient Dynamics and Stability*

As the plant community changes in response to fertilization, we predicted that the initial responses will be transient, and more permanent shifts in vegetation composition will not be evident until later. The surveys in the 5 m × 5 m plots were completed for seven growing seasons, and they permit only an assessment of this prediction. The results of our study verify this prediction. For example, the increase in leaf production in *Mertensia* was apparent only in the third year of the study. *Anemone* initially responded positively to nutrient addition, and it was only after several seasons that its decline became apparent. In part, this may have been due to the long-term nature of the changes being induced by the treatments, such as increased biomass of other species and the gradual accumulation of nutrients in fertilized plots. The fact that initial responses to treatments may not reflect the more permanent long-term responses raises an important issue for experimental field ecology. Grubb (1982) in the United Kingdom and Inouye and Tilman (1995) and Tilman (1988) in Cedar Creek, Minnesota, have demonstrated such immediate "transient dynamics." In each of these cases, early surveys yielded useful information on the potential for short-term interference, but more permanent, stable responses to treatments did not materialize until later. Indeed, at Cedar Creek, changes in species composition were still occurring 10 years after the manipulations had taken place (Inouye and Tilman 1995). Such studies are particularly critical in systems where the species are long-lived and have limited rates of dispersal and establishment. In systems such as the boreal forest understory, it should be expected that new equilibrium conditions would be reached very slowly.

5.4.2 *Impacts of Climatic Warming*

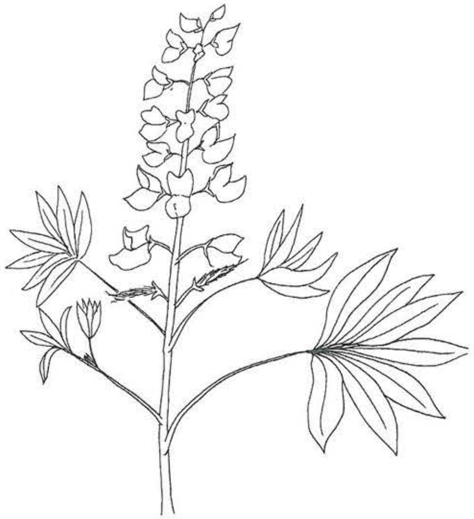
Several authors have suggested that the application of nutrients to northern communities may produce some of the same effects in the plant community that might be caused by global environmental change (Aerts and Berendse 1988, Berendse and Jonasson 1992, Jonasson 1992, Berendse 1994). Global changes such as increasing CO_2 concentrations, increasing deposition of nitrogen and sulfur pollutants, and rising temperatures will have crucial impacts on nutrient cycles, leading to changes in primary production and species composition. Berendse and Jonasson (1992) argue that climate change will increase the supply of nutrients by stimulating decomposition processes and increase the rate of soil carbon accumulation. These changes will, of course, be modified by the interactions between plants and their environment. Reported responses from other systems such as heathland (Aerts and Berendse 1988, McGraw and Chapin 1989) and tundra (Chapin and Shaver 1985, Henry et al. 1986) show that some species will respond strongly to an increased nutrient supply at the expense of others, leading to an increase in biomass but a loss of diversity. In our system we might initially expect that bryophytes, lichens, prostrate growth forms, and low nutrient-requiring species will be suppressed or eliminated by faster growing, more upright clonal species such as the graminoids, *Mertensia paniculata* and *Achillea millefolium* var. *borealis.* Clearly, species and vegetation types with low nutrient-uptake demands will be the most sensitive to the predicted changes. At this stage it is also clear that the shrubs, chiefly *Salix glauca* and *Betula glandulosa,* would increase as well, at least initially, and one could only speculate as to the consequences of this additional food supply on the snowshoe hare cycle.

The majority of the data presented supports the bottom-up hypothesis that herbaceous vegetation standing crop is controlled by nutrient availability alone. With fertilization there was an overall increase in the amount of herbaceous vegetation, especially among the grasses, and a greater nutrient content of vegetation. *Festuca* showed the most dramatic increases in abundance, while *Anemone* and *Lupinus* consistently failed to increase in abundance when fertilized. It is likely that the declines after fertilizer addition for some species are due to competition from the more rapidly growing species. The studies also indicate that the vegetation is not under top-down control and that the impact of mammalian herbivory, primarily by hares, on the vegetation is very low. An effect can be induced when herbivore numbers have been artificially elevated or when the vegetation has been fertilized and the plants are significantly more attractive to hares.

5.5 Summary

Plants in the boreal forest form the physical structure of the community, and they provide the energy and nutrients to the herbivores on which higher trophic levels depend. Our studies focus on the herbaceous vegetation, primarily two grasses, *Festuca altaica* and *Calamagrostis lapponica* and four herbs *Lupinus arcticus, Anemone parviflora, Mertensia paniculata,* and *Achillea millefolium* var. *borealis.* These plants provide a source of relatively high-quality food to the herbivores. Understanding the factors that limit the quantity and the quality of plants is fundamental. Soil nutrients, especially nitrogen, often limit the productivity of boreal forest vegetation and may control vegetation standing crop. Conversely, herbivory may have a direct effect on vegetation quantity and quality. To understand some of the inter-trophic linkages between components of the system, three hypotheses regarding the vegetation were tested: that vegetation was controlled by (1) nutrient availability alone (bottom-up, or donor control), (2) by herbivores alone (top-down control), and (3) by both nutrient availability and herbivores. This involved three major experimental treatments: fertilization, herbivore exclusion, and fertilization plus herbivore exclusion. These treatments allowed us to make specific predictions about changes in plant biomass, or standing crop, under the three different hypotheses. The results support the bottom-up or donor control model for the herbaceous vegetation in the Kluane region of the boreal forest.

Appendix



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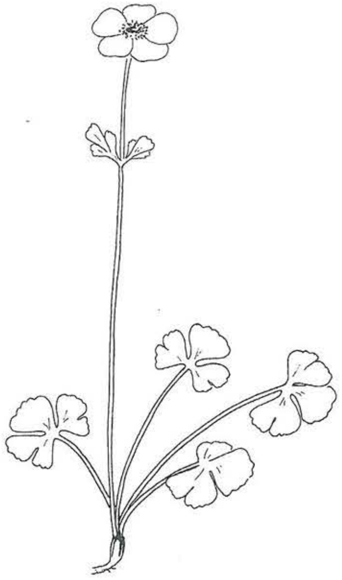

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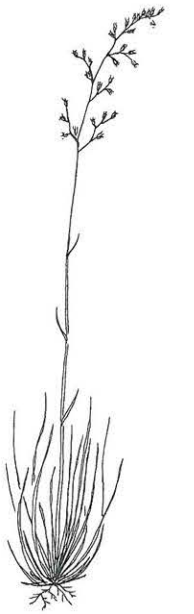

3

4

5

1. Arctic lupine (*Lupinus arcticus*)
2. Northern anemone (*Anemone parviflora*)
3. Northern rough fescue (*Festuca altaica*)
4. Bluebell (*Mertensia paniculata*)
5. Yarrow (*Achillea millefolium*)

Drawings by Shona Ellis.

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