Compensatory Growth Of Three Herbaceous Perennial Species: The Effects of Clipping and Nutrient Availability

by

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ABSTRACT

This study focuses on the active responses of plants to herbivore damage, specifically on the ability of plants to regrow following an episode of herbivory. The Continuum of Responses model (CRM) and the Growth Rate model (GRM) make some conflicting predictions about the effects of soil nutrient availability on compensatory growth by grazed (clipped) plants. A factorial field experiment was conducted to examine the effects of long-term fertilization, short-term fertilization and clipping on the rate of (re)growth and the amount of (re)growth of three herbaceous perennial species, *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*. Plants were collected from areas with different soil nutrient levels (low soil fertility and high soil fertility), planted in a common garden in the field and subjected to one of three simulated herbivory events (0%, 50% and 100% leaf loss) and one of two fertilizing treatments (no fertilizer and fertilizer addition).

Concordant with both models, clipping was detrimental to plant growth which decreased as clipping intensity increased. From the plant's perspective, the impact of herbivory on the proportional leaf area of clipped plants relative to unclipped controls, was independent of short-term fertilization. When biomass was measured, short-term fertilization reduced the compensatory ability of *A. millefolium* and *M. paniculata*, but improved it for *F. altaica*. From the animal's perspective, the impact of herbivory on the absolute size of clipped plants relative to controls was reduced by short-term fertilization, regardless of species and the measure of growth considered. Under natural soil nutrient conditions, *M. paniculata* is more likely to compensate for leaf loss than *A. millefolium* and *F. altaica*.

These results indicate that short-term nutrient availability may affect the compensatory growth of clipped plants, but compensatory responses of the three species studied were only partly consistent with the predictions of the two models.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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INTRODUCTION

The Importance of Herbivory

Explaining the distribution and abundance of species in a community is a fundamental objective of ecology (Krebs 1994, p.3). Species are limited in their abundance and distribution by abiotic factors such as climate (Bonan and Shugart 1989) and disturbance, and by biotic factors such as competition and predation and their relative importance has been the subject of much research (Grime 1977, Oksanen *et al.* 1981, Connell 1983, Menge and Sutherland 1987). Until recently, the importance of herbivory in the shaping of terrestrial plant communities (e.g. grasslands) had been underestimated (Harper 1977, McNaughton 1983) yet consumption of the primary production of terrestrial systems can alter both plant productivity and species composition (Chew 1974, McNaughton 1979), and ultimately the animal species at higher trophic levels.

Plants have traditionally been viewed as passive participants in plant-animal interactions, negatively impacted by the loss of tissue to herbivores (McNaughton 1979). This zoological view of herbivory emphasizes the foraging behaviour of the herbivores and the nutritional value of the food source consumed (Harper 1977, p.385). From the botanical perspective, the amount and type of plant tissue removed and impact on plant fitness is of more importance than the animal which did the biting (Harper 1977, p.386).

The work reported in this thesis focuses on the active responses of plants to herbivore damage, specifically on the ability of plants to regrow following an episode of herbivory. Herbivores generally consume only a portion of their food source (Harper 1977, p.386).

Following herbivory there is potential for the plant to regrow, i.e. to compensate, thereby reducing at least some of the deleterious effects due to tissue loss (McNaughton 1983).

In recent years, compensatory growth by plants after an episode of herbivory has been the source of considerable research effort (e.g. Dyer 1975, McNaughton 1979, Paige and Whitham 1987, Hik *et al.* 1991). Compensation is the growth response of plants following defoliation and can be classified into three levels: undercompensation, equal compensation and overcompensation. Undercompensation occurs when the biomass of a defoliated plant at the end of the growing season is less than the biomass of an undefoliated control plant; equal compensation occurs when the biomass of the defoliated plant equals that of the control; and overcompensation occurs when the biomass of the defoliated plant is greater than that of the control plant (McNaughton 1983). Compensatory ability can refer to the amount of new plant growth (Detling and Painter 1983, Alward and Joern 1993), the rate of plant regrowth (McNaughton 1979, Oesterheld 1992) or to measures of reproductive output (Maun and Cavers 1971, Dyer 1975, Paige and Whitham 1987). Compensation has been applied to individual plants (Chapin and McNaughton 1989, Hicks and Reader 1995), plant populations (Zellmer *et al.* 1993), and to entire plant communities (John and Turkington 1995). In this thesis, compensatory growth refers to rates of regrowth, absolute and proportional amounts of new plant growth, and vegetative reproductive output, of individual plants.

There is much debate in the literature, sometimes contentious, over the actual extent of compensation and whether grazing can improve plant performance (McNaughton 1983, Belsky 1986). The majority of studies show herbivores to be detrimental to the plants they consume, limiting growth (Painter and Detling 1981, Butler and Briske 1988), reproductive output (Inouye 1982, Briggs 1991) and competitive ability of defoliated plants (Harper 1977, pp. 392). Some research, though limited (Bergelson *et al.* 1996), suggests herbivores may benefit the plants they eat by increasing productivity (Owen 1980, McNaughton *et al.* 1983, Cargill and Jeffries 1984) and the production of flowers and seeds (Dyer 1975, Owen and Wiegert 1976, Hendrix 1984, Paige and Whitham 1987).

It was recently proposed that these points of view are not in opposition but are instead, extremes of a continuum of compensatory response (Maschinski and Whitham 1989), and the degree of compensation depends on the environmental context in which herbivory occurs (Whitham *et al.* 1991). When environmental conditions limit plant growth, herbivory is most likely to be detrimental to plant performance, but when conditions for growth are favourable, herbivory may enhance plant growth (Owen 1980, McNaughton 1983, Hendrix 1988, but see Alward and Joern 1993, Hicks and Reader 1995). The effects of a number of factors on plant compensation have been considered including resource availability (Verkaar *et al.* 1986, Bryant 1987, Chapin and McNaughton 1989, Hik and Jeffries 1990), timing of the herbivory event (Maun and Cavers 1971, Oesterheld and McNaughton 1991, Gedge and Maun 1992), defoliation intensity (McNaughton 1979, Painter and Detling 1981), history of previous defoliation (Detling and Painter 1983, Polley and Detling 1988) and the presence of competitors (Lee and Bazazz 1980, Crawley 1990, Weiner 1993). Interactive effects of these factors have also been investigated (e.g. Louda *et al.* 1990, Oksanen 1990, Alward and Joern 1993, Obeso and Grubb 1994).

In addition to environmental factors, compensatory responses may also be dependent on internal plant traits such as growth rate (Hilbert *et al.* 1981, Whitham *et al.* 1991). Plants with high rates of growth will regrow tissues removed by herbivores at a faster rate than plants with slower growth rates. In some cases, herbivory may stimulate increases in plant growth rate that facilitate compensation (Oesterheld 1992).

Several models predict the compensatory responses of plants under a range of conditions. Two of these models consider soil nutrient availability, timing and intensity of defoliation, and plant growth rates, and they make some conflicting predictions about the range of plant compensatory responses to episodes of herbivory.

The Models

(1) **The Continuum of Responses Model (CRM).** *For a single herbivory event, the CRM hypothesizes that a plant is more likely to compensate for tissue loss when soil nutrient availability is high, when competition from neighbours is low, or when the plant is defoliated early in the growing season.*

This is a probabilistic model, derived in part, from the impact of vertebrate grazing on seed production in an herbaceous biennial, *Ipomopsis arizonica* (L.) A. A. Heller (Maschinski and Whitham 1989). The predictions of the model are based on three environmental factors including resource availability, competition from neighbours and timing of defoliation. Soil nutrients facilitate the (re)growth of plant tissues (Begon *et al.* 1990), therefore plants growing in nutrient-rich environments will have an adequate supply for the replacement of lost tissues. In contrast, plants growing in nutrient limited soils will have less nutrients available for regrowth. When neighbours are present, competition for light and nutrients may limit the extent of compensation. Neighbours can shade defoliated plants (Dirzo 1984) or deplete the soil nutrient supply. The later in the season that a herbivory event occurs, the less likely a plant will compensate as the plants have little time to recover before the end of the growing season (Crawley 1983, Oesterheld and McNaughton 1991). Also, as the growing season progresses, soil nutrient supplies become naturally depleted, which could limit the compensatory ability of affected plants (Maschinski and Whitham 1989).

(2) **The Growth Rate Model (GRM)**. *The GRM predicts that the compensatory responses of defoliated plants are dependent on the intensity of the herbivory event and the relative growth rate of the plant prior to tissue loss.*

This is based on a mathematical analysis of plant relative growth rate (RGR) (Hilbert *et al.* 1981). Relative growth rate is the increase in plant material per unit of material per unit time and it represents the efficiency of the plant as a producer of new plant material (Hunt 1982). The predictions of the model are based on the assumption that plants experience an initial increase in RGR of leaf tissue following defoliation. This increase is due, in part, to the increased photosynthetic efficiency of regrowing leaf blades (Bolton and Brown 1980, Caldwell *et al.* 1981). Defoliation affects the photosynthetic capacity of remaining leaves by delaying the natural decline in net photosynthetic rates with aging, or inducing a slight increase (Gifford and Marshall 1973, Hodgkinson 1974). The physiological basis for enhancing photosynthetic capacity is a decrease in the resistance of leaf surfaces to the transfer of CO_2 (Hodgkinson 1974). Growth substances such as cytokinins are associated with stomatal aperture (Jones and Mansfield 1972) and an increase in the concentration of these substances following defoliation may induce stomatal opening, facilitating the transfer of

CO_2 from the atmosphere to chloroplasts. CO_2 is eventually assimilated into structural carbon compounds that are used for plant growth, maintenance and reproduction.

The GRM predicts that when a plant is stressed in some way, and consequently growing slowly compared to its potential relative growth rate, it is most likely to compensate for a herbivory event. Therefore, when plants are growing in low nutrient soils or in the presence of competitors, they will be growing slowly, well below their maximum potential RGR. At the time of defoliation, these plants require only small increases in RGR to achieve a size comparable to undefoliated plants growing in the same soil-nutrient type. In high nutrient, low competition environments, plants will be growing at rates closer to their maximum potential RGR and defoliated plants will require large increases in growth rate to compensate. A non-defoliated plant growing in the same soil, will be growing so rapidly that the defoliated plant cannot easily achieve a comparable final size.

The CRM makes no predictions based on the intensity of defoliation but the GRM predicts that a heavily defoliated plant is less likely to compensate for tissue loss than a lightly defoliated plant. Heavily defoliated individuals require a larger increase in RGR to replace lost tissues and achieve a final size comparable to undefoliated controls.

To summarize, the *GRM predicts that a lightly-defoliated plant, growing slowly in nutrient-poor soils, with competitors, is more likely to compensate for tissue loss.* The *CRM predicts that an early-defoliated plant, growing rapidly in nutrient-rich soils, without competitors, has greater potential for regrowth.* To determine the utility of the CRM and GRM, investigations of the regrowth responses of plants are required. In this thesis, the conflicting predictions of the models with respect to soil nutrient availability are tested. The effect of defoliation intensity on plant regrowth is also addressed. The effects of competition and timing of defoliation are not addressed in this study.

The two major components in this system, the plants and the animals are both affected by tissue consumption. The assessment of compensatory regrowth in fertile versus infertile soils will be dependent on whether we are interested in the plant's perspective or the animal's perspective. Initially, an eaten plant loses a portion of its photosynthesizing tissue and is reduced in size relative to uneaten neighbours but shortly after the herbivory event, the plant will likely regrow. From the plant's perspective, compensatory ability should be measured as the proportional size of the eaten plant relative to uneaten neighbours in the same soil type. Proportional growth is important to a plant as it may determine the outcome of competition for light, for example.

The herbivore gains some nutritional value from the tissue it has eaten, but at the same time reduces the amount of plant biomass available for its next feeding bout. From the animal's perspective, compensatory ability should be assessed using the absolute difference in growth between clipped and unclipped plants in their respective soil types. Absolute growth values are important to the herbivore as they estimate the total amount of plant material available for consumption, and whether or not eating a plant in fertile or infertile soils causes the greatest reduction in available biomass by the end of the growing season. The perspective considered could affect which model is supported, as a significant difference in absolute plant growth between fertile and infertile soils, may not translate into a significant difference in proportional growth.

Only a few studies have attempted to investigate the interactive effects of environmental and internal factors on plant regrowth in the field and the evidence is conflicting. Even fewer have considered the compensatory responses of more than one species at a time (but see Zellmer et al. 1993, Alward and Joern 1993). Most plant compensation studies consider the absolute amount of regrowth and to the best of my knowledge, none have compared the absolute and proportional regrowth responses of plants following defoliation. This provided motivation for the present study, which attempts to quantify the proportional as well as the absolute regrowth responses of three herbaceous plant species, *Achillea millefolium* var. *borealis*, *Festuca altaica* and *Mertensia paniculata*, under different nutrient and clipping regimes.

A factorial field experiment was conducted to examine the effects of species, long-term fertilization, short-term fertilization and clipping on the rate of (re)growth and the amount of (re)growth of individual plants. Plants were collected from areas with different soil nutrient levels (low soil fertility and high soil fertility), planted in a common garden in the field and subjected to one of three possible simulated herbivory events (no clipping, 50% leaf loss and 100% leaf loss) and one of two fertilizing treatments (no fertilizer and fertilizer addition).

The Kluane Boreal Forest Project

This research is part of the Kluane Boreal Forest Ecosystem Project (KBFEP) being carried out near Kluane Lake, Yukon, Canada. The project is a ten-year investigation of the trophic interactions of the food web in the boreal forest to determine how the trophic levels of soils, vegetation, herbivores and predators are affected by each other. The present study investigates one component of this system; quantifying the impact of herbivory on regrowth of herbaceous vegetation.

MATERIALS AND METHODS

Study area

The study was conducted near Kluane Lake, Yukon (61^0 02'N 138^0 22'W), approximately 900m above sea level (Fig.1). The climate of this region is classified as subarctic, continental and is characterized by long, cold winters and short, dry summers (Wahl *et al.* 1987). The mean daily annual temperature is -3.7° C. Average daily temperatures are 10.5° C in June, 12.4° C in July and 10.4° C in August (Douglas 1974, Wahl *et al.* 1987). Annual precipitation of this region averages about 360 mm. The ground is generally snow-covered from mid-October to mid-April, resulting in a short growing season of approximately 100 days. Most plant compensation studies are carried out on herbaceous or woody plants in temperate regions (Obeso 1993); few, if any have been done in areas such as this.

The low temperatures characteristic of the Kluane Lake region contribute to the limited availability of soil nutrients. In mature spruce forests, a thick layer of organic matter, 30cm to 50cm in depth, can cover the mineral substrate but only 2% of it decomposes per year (VanCleve and Alexander 1979). Combined with the acidic nature of spruce leaf litter, low soil temperatures limit the decomposing activity of soil microbes and mineral nutrients remain trapped in a form that is unavailable for plant use (Dyrness *et al.* 1986). Soil nutrients, especially nitrogen, are often limiting to the productivity of boreal forest vegetation (Bonan and Shugart 1989) and previous studies suggest that fertilizer consisting of nitrogen, phosphorous and potassium, is a limiting factor for herbaceous plants at Kluane (Arii 1996, John and Turkington 1995).

The vegetation in this area of the boreal forest, is classified as a closed to open spruce forest community (Douglas 1974). White spruce (*Picea glauca* Voss) is the dominant tree species, interspersed with stands of trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Open areas of shrub habitat are dominated by dwarf birch (*Betula glandulosa* Michx.), grey willow (*Salix glauca* L.) and soapberry (*Sheperdia canadensis* (L.) Nutt.). Herbaceous understorey plants include yarrow (*Achillea millefolium* L. var. *borealis* (Bong.) Farwell, anemone (*Anemone parviflora* Michx.), fescue (*Festuca altaica* Trin.), Arctic lupine (*Lupinus arcticus* S. Wats) and bluebells (*Mertensia paniculata* (Aiton) G. Don).

Herbivores

In the boreal forest, herbaceous vegetation is consumed by a number of small mammalian herbivores including the snowshoe hare (*Lepus americanus* Erxleben), Arctic ground squirrels (*Spermophilus parryi*), red squirrels (*Tamiasciurus hudsonicus*), Northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*). The snowshoe hare, whose population numbers cycle every eight to eleven years, is the dominant herbivore (Krebs et al. 1992). During the summer months, herbaceous vegetation makes up a large proportion of the snowshoe hare diet (Wolff 1978) and when population densities are high, significant amounts of above-ground biomass are consumed. The last snowshoe hare population peak occurred in 1990, followed by a rapid decline in 1991 and 1992. In 1995, the year this study was conducted, the snowshoe hare population size was in the final year of its low numbers.

Study species

The plant species selected for this experiment were *Achillea millefolium* L. var. *borealis* (Bong.) Farwell, *Festuca altaica* Trin., *Mertensia paniculata* (Aiton) G. Don. These herbaceous perennials differ in their relative abundances in the field (John and Turkington 1995) and all are consumed to some extent by snowshoe hares (D. Hik, pers. comm.). *Achillea millefolium* and *Festuca altaica* both ranked highly as food choices in cafeteria-style feeding trials (D. Hik, pers. comm.). Table 1 describes the herbivore consumption patterns for each species and details the responses of each to previous fertilizing and grazing treatments (John and Turkington 1995). Hulten (1968) provides a detailed description of the morphology and distribution of these plants.

Experimental design

The experiment was set up as a four factor split-plot design, with 12 replicate plots of 36 treatment combinations (3 species x 2 long-term fertilizations x 3 clipping intensities x 2 short-term fertilizations). Each plot was a 2.5 m x 2 m area, protected by a three-foot high chicken wire fence (2 cm gauge) to reduce natural herbivory, and cleared of existing vegetation by hand to eliminate any potential effects of competition. To ensure that the fertilizer applications affected only target plants, each plot was divided into two sub-plots (short-term fertilized and unfertilized), separated by a 50cm corridor. The placement of the remaining 18 treatment combinations (3 species x 2 long-term fertilizations x 3 clipping intensities) was randomly assigned within each half (Fig. 3). Each plot contained 36 transplants, 12 individuals of each species, planted approximately 30 cm apart to minimize competitive interactions. With twelve replicates, I used a total of 432 individual transplants for the experiment.

Experimental procedure

Individuals of the experimental species were collected from four sites (A, B, C and D) (Fig. 2) between May 21 and May 27, 1995. Site A had received aerially applied fertilizer, for 5 of the previous nine years. In contrast, plants collected from sites B, C and D were growing under natural conditions of low soil nutrient availability.

To minimize initial size differences for *A. millefolium* and *M. paniculata,* I selected individuals (ramets) with three to five leaves and a visible, central, newly forming leaf. For *F. altaica*, I collected plants with 10 to 15 stems (tillers) and a maximum height of 15 cm to 20 cm. Plants with obvious signs of flowering or previous herbivory were not collected. To minimize initial size differences between the below-ground components of each species, all plants were dug up with an intact soil plug of approximately 112cm^3 (4.5cm in diameter and 7cm deep).

Following collection, plants were transplanted into "uniform garden" plots at Site B. Site B was in the forest, approximately 150m south of the Microwave Tower. The blocks were selected on the basis that all three species occurred there naturally, and that conditions of tree cover, soil moisture and vegetation composition between plots, were visually similar. This provided similar growing conditions for all experimental units. To facilitate successful establishment, plants were watered as needed for 30 days. Dead transplants were replaced until June 4, 1995. Extraneous regrowing vegetation was removed from the blocks every week.

Treatments

a) Long-term fertilization: Plants of the three species were collected from sites with (site A) and without a history of fertilization (sites B, C and D) as discussed above.

b) Short-term fertilization: During the 45-day period following clipping, half of all plants received a weekly application of water-soluble, N-P-K fertilizer (20:20:20), applied at the recommended rate for outdoor plants of 2g per 250ml per plant, and half received a weekly application of 250ml of water with no fertilizer.

c) Clipping intensity: From May 31, plants were given 30 days to establish and grow and then clipping treatments were applied. One third of transplants had 100% of their leaf area removed, one third had 50% removed and the remaining one third were not clipped. To simulate the natural pattern of snowshoe hare grazing for *A. millefolium* and *M. paniculata* plants, leaves were clipped with scissors at the base of the petiole (Fig. 4). When an odd number of leaves was present for the 50% clipping treatment, I removed the upper half of the leaf blade of the odd numbered leaf. For *F. altaica*, tillers were clipped to 2cm above ground-level. All clipped pieces were removed from the plots, dried and weighed. Forty-five days after clipping, all plants were carefully removed from the blocks using a trowel. Plant material was separated into above-ground and below-ground components, dried and weighed.

Dependent variables

To test the conflicting predictions of the CRM and GRM by determining the effect of experimental treatments on plant performance, I measured and calculated a number of dependent variables for each transplant. To compare the animal and plant perspectives, the variables measured are classified into two main categories. For the plant-view, I consider proportional differences in the size of clipped plants relative to unclipped controls, and for the animal-view I consider the absolute differences in plant size due to clipping.

Measures of leaf area and plant biomass address the impact of herbivory in the short-term, whereas measures of vegetative reproduction give an indication of the long-term effect of herbivory on plants (i.e. fitness). For this reason, results for reproductive variables are placed in a separate category.

I. Plant-view

(a) Leaf area

For the duration of the experiment, total leaf area was measured every two weeks for each individual plant, providing a non-destructive measure of plant growth over time.

(1) Relative growth rate (RGR) of leaf area (per day) following clipping. Rate of growth following herbivory may be important to plants growing in seasonally restricted habitats such as Kluane. Leaf tissue is required for photosynthesis, which generates energy reserves for growth, reproduction and overwinter storage.

(2) Proportion of post-clipping growth of leaf area of clipped plants relative to unclipped controls. This measures the amount of tissue that a plant was able to replace before the end of the growing season, indicative of its regrowth ability.

(3) Proportion of final leaf area (cm^2) of clipped plants relative to unclipped controls.

This measure is important for the plant as it indicates how much leaf area clipped plants grow by the end of the growing season, compared to unclipped neighbours.

(b) Biomass

Biomass measurements were taken at the end of the growing season, and included the mass of leaves as well as the mass of petioles and supporting stems.

(4) Proportion of above-ground biomass of clipped plants relative to unclipped controls. This measure is important for plants as it indicates how much green biomass a clipped plant can grow by the end of the growing season to potentially compete with unclipped neighbours.

(5) Proportion of below-ground biomass of clipped plants relative to unclipped controls. This measure is important for plants as it indicates how much root biomass a clipped plant can grow by the end of the growing season, compared to unclipped neighbours.

(6) Proportion of total biomass of clipped plants relative to unclipped controls.

(7) Ratio of above-ground biomass to total biomass. This measure of the amount of shoot compared to total plant, demonstrates a plant's energy allocation strategy following clipping.

Variables (2) through (6) were calculated by dividing 50% and 100%-clipping values by the values for respective unclipped controls, for all individual plants.

II. Herbivore-view

(a) Leaf area

(1) Post-clipping growth (cm^2). This measure is important to the herbivore, as it

represents the amount of biomass that is replaced by the plant following the herbivory event. Any regrowth in leaf area is new tissue available for consumption. New tissue is often low in fibre and higher in nitrogen than older plant leaves, providing herbivores with a good source of forage (Glover *et al.* 1960).

(2) Final leaf area (cm^2). This measure gives the total amount of leaf area available for consumption by the end of the growing season.

(b) Biomass

(3) Above-ground biomass (g) is important to the herbivore as it estimates the total amount of green biomass available for consumption.

(4) Below-ground biomass (g) is not of direct importance to the herbivore, but absolute changes in root size are of direct relevance to energy allocation in the plants being eaten, and so are included here.

(5) Total biomass (g).

III. Vegetative reproduction

Increases or decreases in biomass alone cannot be used as critical evidence for determining the impact of herbivores on plants. Whitham *et al.* (1991) propose that reproductive output is an important variable to consider in this respect. Due to the difficulty in obtaining lifetime fitness measures, most investigations, including the present study, consider only one reproductive season (see review by Obeso 1993). Vegetative reproduction is the most prominent method of reproduction in all of the study species.

(1) Vegetative reproduction (# of ramets or tillers). This measure was included to approximate plant fitness, because ramet and tiller counts are a direct measure of reproductive output.

(2) Proportion of ramet leaf area : final leaf area for *A. millefolium* and *M. paniculata*. This measures the amount of biomass that a plant allocates to parent plant regrowth compared to growth of vegetatively produced offspring. Data for *F. altaica* are not available.

Calculation of leaf area

To calculate final leaf area for *F. altaica*, the following equation is used:

$$\text{Final leaf area (cm}^2\text{)} = \sum (L \times W) \qquad [1]$$

Where L and W are the length and width of individual leaves respectively. W is set at an average width of 0.02 cm ($n = 20$).

Due to the shape of the leaves of *M. paniculata* and *A. millefolium*, final leaf area could not be estimated using (L x W) alone. For both species, a leaf area meter (Hyan-Walls LI-356) was used to measure the area of a subsample of the experimental leaves ($n = 35$ and $n = 51$ respectively). To determine the best predictor of leaf area for each species, area was regressed against three leaf-size variables; L, W and (L x W). Leaf length explained the greatest amount of variation in area for *M. paniculata* leaves ($R^2 = 0.82$, $p < 0.001$), and (L x W) was the best predictor of leaf area for *A. millefolium* ($R^2 = 0.85$, $p < 0.001$). Equations [2] and [3] were then used to estimate final leaf area of *M. paniculata* and *A. millefolium* respectively:

$$\text{Final leaf area (cm}^2\text{)} = \sum (4.16 \times L - 9.18) \qquad [2]$$

$$\text{Final leaf area (cm}^2\text{)} = \sum (0.25 \times (L \times W) + 0.442)) \quad [3]$$

Calculation of relative growth rate (RGR)

Mean relative growth rate was calculated over the 15 days of post-clipping growth, when plants were most likely to experience the highest growth rate increases (Hilbert *et al.* 1981). RGR was calculated as follows:

$$RGR = (\ln LA_{45} - \ln LA_{30}) / 15 \text{ days} \quad [4]$$

Where LA_{45} and LA_{30} are total leaf areas per plant on day 30 and day 45 of the experiment, respectively. Day 30 was the day that the clipping treatments were imposed on the plants and LA_{30} was the measure of leaf area per plant immediately following clipping.

Statistical analysis

For each of the eight variables, a four-way ANOVA was used to test for main effects and for interactions of species, long-term fertilization, clipping intensity and short-term fertilizer addition. The use of a split-plot design imposed restrictions on randomization of the short-term fertilization treatment. Therefore, analysis of this treatment effect used the mean square error of the block x short-term fertilization term and its corresponding degrees of freedom to calculate the F-ratio denominator. Data were analyzed using the general linear models procedure in SAS (SAS Institute Inc. 1988). Significance testing ($p < 0.05$) used type III sum of squares. Orthogonal contrasts were used to compare the combined effects of selected treatment means (Little and Hills 1978). Prior to analysis, data were checked for normality and homogeneity of variances. Proportional data for post-clipping growth, final leaf area, below-ground and total biomass were log (x +1) transformed, reducing heteroscedasticity. The arcsine transformation was not used for these data as the proportions were often greater than one (Zar 1984). Vegetative reproduction data were log transformed, and above-ground biomass : total biomass ratios, and ramet leaf area : final leaf area ratios were arcsine square-root-transformed. Results are graphed as untransformed means. Orthogonal contrasting results are extensive and have therefore been placed in appendices. A key to the orthogonal contrast treatment combinations that were analyzed is found Appendix 13. For *F. altaica* and *M. paniculata*, mortality during the pre-treatment period reduced the sample sizes for some of the treatment combinations (Table 2).

RESULTS

I. PLANT VIEW

(a) LEAF AREA

Relative growth rate (RGR)

The relative growth rate of leaf area was greater for clipped plants than for unclipped plants (Fig. 5). Planned contrasts of clipping means, showed that 50% leaf loss increased RGR significantly more than 0% leaf loss ($F = 20.66$, $P = 0.0001$) and 100% leaf loss increased RGR significantly more than the 50% leaf loss treatment ($F = 1403.76$, $P = 0.0001$) (Appendix 1b).

Short-term fertilization caused an increase in RGR, but the difference in RGR between plants with 0% and 100% leaf loss was significantly greater for unfertilized plants than for fertilized plants ($F = 8.22$, $P = 0.0044$) (Fig.6; Appendix 1b). This increase was greater for *M. paniculata* than for both *F. altaica* ($F = 6.66$, $P = 0.0103$) and *A. millefolium* ($F = 8.37$, $P = 0.0041$), which accounts for the significant interaction of clipping, fertilizing and species effects in the ANOVA (Table 3).

Long-term fertilization also caused an increase in RGR (Fig.7). For *F. altaica* and *M. paniculata*, the increase in RGR caused by 100% leaf loss was greater for unfertilized plants than for fertilized plants (Fig. 7b, 7c), but this was reversed for *A. millefolium* (Fig. 7a). The response of *A. millefolium* differed significantly from the response of *M. paniculata* ($F = 4.00$, $P = 0.0463$) and *F. altaica* ($F = 8.48$, $P = 0.0038$), which accounts for the significant clipping x history x species interaction in the ANOVA (Table 3).

The increase in RGR caused by short-term fertilization was significantly greater for plants that had not received long-term fertilization (Fig. 8). The magnitude of this difference was significantly greater for *M. paniculata* than for *A. millefolium* ($F = 8.65$, $P = 0.0035$), which accounts for the significant interaction of fertilizing x history x species, in the ANOVA (Table 3), and these were not different form *F. altaica* ($F = 2.21$, $P = 0.1382$).

Post-clipping growth

With short-term fertilization, clipped plants grew 37% less than unclipped controls in the 45 days following clipping (Fig. 9). Unfertilized clipped plants regrew significantly more, with 180% more leaf area than unclipped controls in the same time span (Table 4). The 50% leaf loss and 100% leaf loss treatments did not differ in their effect on the proportional size of clipped plants relative to controls. Also, there were no significant differences between species.

Final leaf area

In both short-term fertilized and unfertilized plants of all species, 50% leaf loss reduced plant size by approximately 25%, and 100% leaf loss reduced plant size by 65% (Fig. 10; Table 5). Long-term fertilization did not have as consistent an effect. With 50% leaf loss, long-term fertilization decreased the proportional size of *A. millefolium*, and increased it for *F. altaica* and *M. paniculata*. With 100% leaf loss, long-term fertilization increased proportional size of *A. millefolium* and *M. paniculata*, but decreased it for *F. altaica* (Fig. 11). The response of *A. millefolium* differed significantly from the response of *F. altaica* (F =

4.73, P = 0.0309) but not *M. paniculata* (F = 3.11, P = 0.0792), which accounts for the significant effect of clipping, long-term fertilization and species in the ANOVA (Table 5). The orthogonal contrast summary for this variable is found in Appendix 2.

(b) BIOMASS

Above-ground biomass

Relative to unclipped controls, the proportional biomass of 100%-clipped plants was less than the proportional biomass of 50%-clipped plants (Fig. 12). For *F. altaica*, short-term fertilization increased the proportional size of clipped plants relative to controls (Fig. 12). This differed significantly from the responses of both *M. paniculata* and *A. millefolium* (F= 5.08, P = 0.0253), where short-term fertilization reduced the proportional size of both 50% and 100%-clipped plants. This accounts for the significant interaction of clipping, species and short-term fertilization in the ANOVA (Table 6). For all species, long-term fertilization significantly reduced the proportional biomass of clipped plants relative to unclipped controls (Fig. 13; Table 6). The orthogonal contrast summary for this variable is found in Appendix 3.

Below-ground biomass

For 50% and 100% leaf loss, the proportional reduction in below-ground biomass of clipped plants relative to unclipped controls, was not significantly different (Table 7). For *A. millefolium* and *M. paniculata*, short-term fertilization decreased the proportional size of unclipped plants (Fig. 14). This response differed significantly from *F. altaica*, where short-term fertilization increased the proportional size of below-ground parts relative to unclipped controls (F = 6.55, P = 0.0112). The orthogonal contrast summary for this variable is found in Appendix 4.

Total biomass

Relative to unclipped controls, 100% leaf loss reduced the proportional size of all plants, significantly more than 50% leaf loss (Fig. 15; Table 8). Similar to the results for below-ground biomass, short-term fertilization decreased the proportional size of unclipped plants for *A. millefolium* and *M. paniculata*, and increased the proportional size for *F. altaica* (F = 7.17, P = 0.008) (Fig. 16). The orthogonal contrast summary for this variable is found in Appendix 5.

Ratio of above-ground biomass : total biomass (AGB:TB)

The ratio of above-ground biomass to total biomass was significantly reduced by 50% leaf loss (F = 4.03, P = 0.0454) and 100% leaf loss (F = 56.03, P = 0.0001) (Fig. 17), for all treatment combinations. Short-term fertilization significantly increased the AGB:TB ratio (Fig. 18; Table 9), but did not significantly interact with any other treatments.

Long-term fertilization caused an increase in AGB:TB for *A. millefolium* and *M. paniculata* and a slight decrease for *F. altaica* (F = 17.85, P = 0.0001) (Fig. 19). The difference in the ratio caused by long-term fertilization was significantly greater for *A. millefolium* and *M. paniculata* than for *F. altaica* (F = 17.85, P = 0.0001) (Fig. 19), which accounts for the significant species x long-term fertilization effect in the ANOVA (Table 9). The orthogonal contrast summary for this variable is found in Appendix 6.

II. ANIMAL VIEW

(a) LEAF AREA

Post-clipping growth

The change in post-clipping growth caused by 100% leaf loss was significantly greater for short-term fertilized than for unfertilized plants ($F = 19.92$, $P = 0.0001$). The 100% leaf loss reduced post-clipping growth for all short-term fertilized plants ($F = 8.44$, $P = 0.0039$), caused a slight reduction in unfertilized *A. millefolium* and *F. altaica* (Fig. 20a, b), and an increase in *M. paniculata* (Fig. 20c). The difference in post-clipping growth between 0% and 100% leaf loss, in fertilized compared to unfertilized plots, was significantly greater for *M. paniculata* than for *A. millefolium* ($F = 4.32$, $P = 0.0385$). The response of *F. altaica* did not differ significantly from the responses of either *A. millefolium* ($F = 1.03$, $P = 0.3112$) or *M. paniculata* ($F = 1.05$, $P = 0.3052$).

Long-term fertilization did not significantly interact with the clipping treatments, but increased post-clipping growth for each of three species (Fig. 21). This increase was significantly greater for *M. paniculata* than for *A. millefolium* ($F = 12.12$, $P = 0.0006$) and for *F. altaica* ($F = 10.09$, $P = 0.0016$), which accounts for the significant effect of long-term fertilization x species in the ANOVA (Table 10). The orthogonal contrast summary for this variable is found in Appendix 7.

Final leaf area

The response of final leaf area to clipping was similar to the response of post-clipping growth (Table 11a). Contingent on the interaction of short-term fertilization and species, the difference in final leaf area between 0% and 100% leaf loss was significantly greater for fertilized than for unfertilized plants (F = 19.92, P = 0.0001) (Fig. 22). This difference was significantly greater for *M. paniculata* than for *A. millefolium* (F = 4.51, P = 0.0344). The response of *F. altaica* did not differ significantly from the responses of either *A. millefolium* (F = 0.58, P = 0.4476) or *M. paniculata* (F = 1.74, P = 0.1883) (Table 11b).

Long-term fertilization did not significantly interact with the clipping treatments but did so with species (Table 11a). Long-term fertilization caused an increase in final leaf area that was significantly greater for *M. paniculata* than for *A. millefolium* (F = 11.31, P = 0.0009) (Fig. 23a, c). For *F. altaica*, long-term fertilization caused a decrease in leaf area (Fig. 23b). The orthogonal contrast summary for this variable is found in Appendix 8.

(b) BIOMASS

Above-ground biomass

In 17 of the 18 possible long-term fertilization x species x short-term fertilization combinations, above-ground biomass failed to compensate for the effects of clipping (Fig. 24; Table 12a). Only one case, long-term fertilized *M. paniculata* with 50% leaf loss, had a higher above-ground biomass than unclipped controls. This increase was not significant as 100% leaf loss (F = 5.54, P = 0.0191) accounted for the significant interaction of long-term fertilization and clipping in the ANOVA (Table 12a).

For each species, the difference in above-ground biomass between 0% and 100% leaf loss was significantly greater for both short-term fertilized (F = 26.7, P = 0.0001) (Fig. 25) and long-term fertilized plants (F = 5.54, P = 0.0191) (Fig. 26; Table 12b).

Short-term fertilization increased above-ground biomass for all treatment combinations (Fig. 24). For *A. millefolium* and *M. paniculata*, the increase in biomass was greater for plants that had received long-term fertilization (Fig. 24a, c). For *F. altaica*, this only occurred under 50% leaf loss (Fig. 24b). The response of *F. altaica* differed significantly from the response of the dicots (F = 4.87, P = 0.0279). The biomass responses of *A. millefolium* and *M. paniculata* were not different (F = 0.15, P = 0.6967) (Table 12a). The orthogonal contrast summary for this variable is found in Appendix 9.

Below-ground biomass

Below-ground biomass was reduced significantly more by 100% leaf loss than by 50% leaf loss, for all 12 of the species x short-term fertilization x long-term fertilization combinations (F = 4.57, P = 0.0332) (Fig. 27; Table 13a). With 50% leaf loss, the difference in below-ground biomass between clipped and unclipped plants depended on the interaction of short-term fertilization, long-term fertilization and species (Table 13a). The magnitude and direction of the change in below-ground biomass was significantly different for *F. altaica* compared to *A. millefolium* and *M. paniculata* (F = 10.04, P = 0.0017), which accounts for the significant four-way interaction in the ANOVA (Table 13b). The orthogonal contrast summary for this variable is found in Appendix 10.

Total biomass

After 45 days of regrowth, none of the clipped plants were able to achieve the same final total biomass as unclipped control plants (Fig. 28). The reduction in total biomass was significantly greater for *F. altaica* than for *M. paniculata* (F = 4.71, P = 0.0306), though neither of these were different from *A. millefolium* (Fig. 28). With short-term fertilization the reduction in total biomass due to clipping was significantly increased for all species (F = 5.84, P = 0.0161) (Fig. 29).

With the 50% leaf loss treatment, the change in total biomass was dependent on the interaction of long-term and short-term fertilization, but not species. The difference between 0% and 50% leaf loss was also significantly greater when plants received short-term fertilization (F = 6.7, P = 0.01) (Fig. 29). For plants that had not received short-term fertilization but had received long-term fertilization, 50% leaf loss caused a slight increase in total biomass compared to controls (Fig. 29). In contrast, for plants that had received no long-term fertilization, total biomass was reduced when clipped. The difference in magnitude and direction of change for these responses was significantly different (F = 5.04, P = 0.0254).

Short-term fertilization increased the total biomass in five of the six possible species by long-term fertilization comparisons (Fig. 30). For *F. altaica* with long-term fertilization, short-term fertilization decreased total biomass, differing significantly from the increases in biomass of *A. millefolium* and *M. paniculata* (F = 6.09, P = 0.0141). This accounts for the significant interaction of species, long-term and short-term fertilization in the ANOVA (Table 14). The orthogonal contrast summary for this variable is found in Appendix 11.

III. VEGETATIVE REPRODUCTION

Number of offspring (ramets and tillers)

Ramets are the units of vegetative reproduction for *M. paniculata* and *A. millefolium* and tillers for *F. altaica*. Vegetative reproduction was reduced by both 50% and 100% leaf loss from the parent plant (Fig. 31). The reduction in reproduction caused by 50% leaf loss was significantly greater for short-term fertilized than for unfertilized plants ($F = 2.2$, $P = 0.0438$). Similarly, the reduction in reproduction caused by 100% leaf loss was significantly greater when plants were fertilized ($F = 4.31$, $P = 0.0387$). The 100%-clipping alone, reduced vegetative reproduction by an average of 0.6 offspring and with short-term fertilization clipping caused an average reduction of 3.17 offspring. This accounts for the significant interaction of clipping and short-term fertilization in the ANOVA (Table 15).

All species responded positively to short-term fertilization by doubling the number of offspring produced. For *F. altaica*, the number of tillers increased by six, and for *A. millefolium* and *M. paniculata* the number of ramets increased by 1.7 and two, respectively (Fig. 32). The increase was significantly greater for *F. altaica,* than *M. paniculata* ($F = 38.46$, $P = 0.0001$), and was significantly greater for *M. paniculata* than for *A. millefolium* ($F = 4.17$, $P = 0.0419$), accounting for the significant interaction effect of species x short-term fertilization in the ANOVA (Table 15).

For *F. altaica* and *M. paniculata*, long-term fertilization had a similar effect on reproduction as the short-term fertilization treatment. That is, the decrease in reproduction caused by 100% leaf loss was greater for long-term fertilized plants than for unfertilized plants (Fig. 33b, 33c). The responses of *F. altaica* and *M. paniculata* did not differ ($F = 1.64$, $P = 0.2008$). In contrast, for *A. millefolium* the decrease in vegetative reproduction was reduced by long-term fertilization (Fig. 33a). The response of *A. millefolium* differed significantly from the response of *F. altaica* ($F = 5.02$, $P = 0.0257$), but not significantly from the response of *M. paniculata* (F = 0.85, P = 0.3584). The orthogonal contrast summary for this variable is found in Appendix 12.

Proportion of total plant leaf area allocated to ramets

For *A. millefolium* and *M. paniculata,* 100% leaf loss of the parent plant, always reduced the proportion of total plant leaf area that was allocated to ramets (F = 11.15, P = 0.0011) (Fig. 34; Table 16). On average, *A. millefolium* invested more of its total leaf area into ramets than *M. paniculata* (Fig. 34). Short-term fertilization did not significantly effect the leaf area proportions for either species (F = 0.73, P = 0.4104). Long-term fertilization increased the proportion of final plant leaf area that was allocated to ramets. This increase was significantly greater for *A. millefolium* than for *M. paniculata* (F = 13.26, P = 0.0004) (Table 16), which accounts for the significant interaction of species and long-term fertilization effects in the ANOVA.

DISCUSSION

Interactions such as predation and herbivory are generally thought to have negative impacts on the performance of prey and plants respectively (McCollum and Van Bushkirk 1996). However, because of the nature of herbivory, in which the plant that is eaten does not always die, there exists the potential for individuals to regrow, compensating for lost tissue (McNaughton 1983). The question of whether and under what circumstances compensation is most likely to occur, has prompted much debate in the plant-animal interactions literature (Belsky 1986, McNaughton 1986, Whitham *et al.* 1991). The purpose of this study therefore, was to evaluate the ability of two conflicting hypotheses to predict the regrowth abilities of three herbaceous plant species under various environmental conditions.

The Continuum of Responses Model (Maschinski and Whitham 1989) and the Growth Rate Model (Hilbert *et al.* 1981), both predict decreased plant performance following a herbivory event. The conflicting predictions of the two models concern responses along gradients of nutrient availability. Hilbert *et al.* (1981) predict that herbivory is more detrimental to plant performance if it occurs in high-nutrient soils. In contrast, Maschinski and Whitham (1989) propose that plant performance suffers more when herbivory occurs in low-nutrient soils.

Concordant with both hypotheses, I observed that clipping was generally detrimental to plant performance in the three species examined. Plant performance decreased as clipping intensity increased, supporting the predictions of the GRM. The CRM makes no predictions with respect to clipping intensity. These observations were independent of the measure (e.g.

biomass) considered, and were consistent with the findings of other studies (e.g. Olson and Richards 1988, Obeso and Grubb 1994). Although clipping had negative effects on plant performance, all plants compensated for tissue loss to some extent. However, the response following clipping was contingent upon the species and the soil fertilization level considered. Furthermore, conclusions about the extent of damage caused by herbivory in different soil types depended on whether the plant or animal perspective was considered. In the following sections, I address the effects of leaf removal on compensation of leaf area, biomass, and vegetative reproduction. I will then synthesize the results, addressing the impact of regrowth on the boreal forest plant community and will make recommendations for future models.

I. PLANT VIEW

Leaf area

Following clipping, all three species experienced an increase in relative growth rate in leaf area and this is consistent with previous studies (e.g. Cargill and Jeffries 1984, Oesterheld and McNaughton 1991, Oesterheld 1992). Consistent with the assumptions of the GRM, the increase in RGR was greater in unfertilized soils compared to fertilized soils and this translated into a doubling of the post-clipping growth of clipped plants compared to unclipped controls. In fertilized soils, the unclipped plants grew only 40% more than clipped plants following defoliation.

By the end of the experiment the dramatic differences in RGR and post-clipping growth between fertilized soils and unfertilized soils did not translate into improved compensatory ability for any of the species. Plants that lost 50% of their leaf area ended up being approximately 25% smaller than unclipped plants, in both short-term fertilized and unfertilized soils. Similarly, plants that lost 100% of their leaf area ended up being approximately 60% smaller than unclipped plants in both soil types. Therefore, from the plant's perspective, it did not matter whether herbivory occurred in fertilized or unfertilized areas. The percent reduction in clipped plant size was the same for both.

Long-term fertilization did significantly affect the proportional size of clipped plants relative to unclipped controls. Pre-clipping resource availability caused more variation in compensatory ability than post-clipping conditions, interacting differently with species and clipping intensity. Post-clipping resource availability ultimately dictated the extent of plant compensation, as there were no significant short-term by long-term fertilization interactions. This is consistent with the predictions of Escarré *et al.* (1996), who hypothesized that current soil nutrient conditions strongly affect the regrowth ability of defoliated plants.

Neither the CRM nor the GRM predict that compensation may be independent of soil nutrient availability. Consequently, final leaf area results are inconsistent with the predictions of both models. Similar findings were reported by Briggs (1991), Honkanen and Haukioja (1994) and Hicks and Reader (1995). It is possible that a resource other than soil nutrients (e.g. water availability) is more limiting to the regrowth of leaf area in boreal forest plants, but this would require additional experimentation. At present, future models need to allow for nutrient-independent compensatory responses of plants to grazing, perhaps by specifying the minimum amount of variation in soil resource availability required to affect the compensatory response of a species.

Biomass

When compensatory growth responses to clipping were measured in terms of biomass rather than leaf area, results provided some support for both models.

Under natural soil nutrient conditions, graphical results suggest that *M. paniculata* is more likely to compensate for leaf loss than *A. millefolium*, which is more likely to compensate than *F. altaica*. Under fertilized conditions, the compensatory ability of *F. altaica* was dramatically improved. This result is consistent with predictions of the CRM and also with results of many previous studies (e.g. McNaughton and Chapin 1985, Chapin and McNaughton 1989, Westoby 1989). Serengeti grass species show well developed compensatory growth following defoliation in high-nutrient soils. Natural soil fertility levels are extremely high in the Serengeti (McNaughton and Georgiadis 1986) and the grasses lose their potential for compensatory growth when soil nutrients are deficient (Chapin and McNaughton 1989). For *M. paniculata* and *A. millefolium*, short-term fertilization reduced the proportional biomass of plants relative to unclipped controls, supporting the predictions of the GRM. This pattern of compensation occurred under moderate herbivory for above-ground biomass, with a similar but less dramatic result following severe defoliation. For below-ground and total biomass, *F. altaica* responded positively to fertilization, regardless of defoliation intensity.

The regrowth of above-ground biomass came at the expense of below-ground parts for all species, which is consistent with results of Ryle and Powell (1975) and Detling *et al.* (1979). In perennial plants, defoliation generally results in an inhibition or even a decrease in root growth (Chapin *et al.* 1987). The reduction in root mass following defoliation could have been due to the net export of carbon from roots to shoots, or to preferential allocation of current photosynthetic products to new leaf growth. The physiological basis for these results was not investigated in this study, but in perennial plants where roots persist year after year, it is not unusual for photosynthates to be stored in roots and used for shoot growth (Dittmer 1971). In Serengeti grasses, the regrowth of leaves following defoliation strongly reduces nutrient reserves in the crown and roots (McNaughton *et al.* 1983).

Similar to other studies (e.g. Cartwright and Kok 1990, but see Schierenbeck *et al.* 1994, Mauricio *et al.* 1993), I found that allocation of biomass to above-ground parts decreased with clipping. For a reduction in both root size and shoot allocation to occur, it is likely that root carbon reserves are initially implemented in shoot regrowth and when new leaves begin to photosynthesize, more photosynthates than usual are diverted into roots. This is most likely to occur following severe defoliation, when all photosynthesizing leaves are removed and root carbon stores would have to be implemented in regrowth. Following tissue loss, a plant may invest more resources into below-ground parts, as above-ground structures would be exposed to subsequent herbivore attacks.

Short-term fertilization caused an increase in allocation to shoots for all species. In *F. altaica*, where fertilization also minimized root reduction following clipping, the use of root reserves may have stopped when additional nutrients were provided. This was not the case for *M. paniculata* or *A. millefolium*. The ability of fertilization to improve regrowth of shoot, root and total biomass of *F. altaica*, is consistent with the results of John and Turkington (1995), where *F. altaica* converted added nutrients into biomass more rapidly than did *M. paniculata* and *A. millefolium*.

II. ANIMAL VIEW

From the animal's perspective, tissue consumption was more detrimental to the final leaf area, above-ground and total biomass if it occurred in fertilized areas. In contrast with results of proportional comparisons, an episode of severe defoliation in fertilized plants caused a greater reduction in available plant tissue, than defoliation in unfertilized plants. Results were independent of species and are all consistent with predictions of the GRM.

When the currency is available forage, regrowth results suggest that a bite taken from a fertilized plant does more damage than a bite of the same size taken from an unfertilized plant. The bite taken from a fertilized plant results in a greater loss of tissue available for consumption at the end of the plant's growing season. The herbivores may not be detrimentally affected by this response, as the initial amount of biomass available for consumption is generally greater on highly fertile soils (John and Turkington 1995), and plants growing here generally have higher concentrations of nutrients per gram of plant tissue (Chapin and McNaughton 1989).

Hungate (1975) reported that ruminants consumed larger amounts of highly nutritious grasses compared to lower quality forage. Therefore, if the density and consumption rates of snowshoe hares increase on a fertile site, the food source could be depleted faster than it would on an infertile site where density and consumption rates would be lower. Herbaceous vegetation makes up a large proportion of the snowshoe hare summer diet (Wolff 1978). If summer foods are in short supply, alternative food sources, such as dwarf birch and grey willow that are generally consumed in the winter, may be consumed earlier in the season.

III. VEGETATIVE REPRODUCTION

Clipping has been found to increase (e.g. Paige and Whitham 1987, Maschinski and Whitham 1989), decrease (e.g. Inouye 1982, Louda 1984) or have no effect on the reproductive output of plants (e.g. Lee and Bazzaz 1980). In the present study, leaf loss had a negative impact on the number of offspring produced by the three species as well as the proportion of total leaf area that was allocated to offspring in *A. millefolium* and *M. paniculata*. The plant energy budget that was to be used for reproduction, was most likely reallocated to regrowth of the parent plant, once tissues were removed. Previous studies have found the balance between vegetative and reproductive tissues to be influenced by herbivory in a number of ways (see McNaughton 1979).

The CRM did not successfully predict plant response to variation in soil nutrient availability. Results showed that clipping caused a stronger decrease in number of offspring for short-term fertilized plants, compared to unfertilized controls. Similar results were reported by Mutikainen and Walls (1995), where fertilization caused a greater decrease in flower mass of a defoliated annual nettle (*Urtica urens*).

Long-term fertilization increased the compensatory ability of one species, *A. millefolium*, which provides some support for the CRM. Long-term fertilization of *A. millefolium* also increased allocation of total plant leaf area to ramets suggesting additional nutrients may be stored in rhizomes and used for ramet production. Short-term fertilization increased the number of ramets produced, the size of the offspring and the size of the parent plant, but had no effect on the proportion of total plant leaf area that was allocated to offspring. This suggests that allocation patterns are hard-wired by the availability of nutrients to which a plant has become adapted. Addition of extra nutrients increases both parent plant size and offspring size, but does not affect the allocation pattern.

In terms of absolute biomass and leaf area, *A. millefolium* was a consistently inferior compensator than *M. paniculata*, but produced consistently more offspring than *M. paniculata* under all treatment conditions. This suggests that *A. millefolium* may be hardwired for clone expansion, reducing its compensatory ability. Clone expansion could be an avoidance strategy, where the production of many small plants are not as attractive to herbivores as a single larger adult.

SPECIES

Results show that the amount of compensatory growth following clipping can be species-dependent. Under natural conditions of low soil nutrient availability, *M. paniculata* was more likely to compensate for herbivory, followed by *A. millefolium* and then *F. altaica*. This order of decreasing compensatory ability occurred for absolute leaf area variables, and proportional above-ground and total biomass variables. It suggests that *M. paniculata* is more resilient to herbivory than both *A. millefolium* and *F. altaica* which could be beneficial to its performance during the high phase of the snowshoe hare population cycle. It is possible that the faster relative growth rate and subsequent compensation of *M. paniculata*, was due to a more concentrated carbon supply in its roots or a more efficient way to export it. This species compensated the most above-ground biomass, while sacrificing the least below-ground biomass.

Escarré *et al.* (1996) found that, among three monocarpic composite forbs, the species that branched on the upper half of its flowering stem, recovered from leaf loss more than the species which branched from the base upwards. The extent to which a plant compensates for tissue loss may depend on species traits such as phenology and architecture (Whitham *et al.* 1991). Structural differences (Table 1) were not included in the present study but may have had an effect on the differences in compensatory ability between species.

The question of whether regrowth ability can help to explain the relative abundance of species in the Kluane boreal forest can be addressed by combining my data with data from long-term herbivore exclosure and fertilization experiments of John and Turkington (1995). In unfertilized soils, John and Turkington (1995) found that the presence of herbivores reduced percent cover of *A. millefolium*, *F. altaica* and *M. paniculata*, by 1%, 0% and 0% respectively. In fertilized soils however, the presence of herbivores reduced percent cover by 3%, 5% and 4% respectively. Such changes were insignificant and concur with some results of the present study, where proportional data showed no significant effect of fertilization or species on changes in leaf area with clipping. It should be cautioned that changes in percent cover could be attributed to changes in the size of individual plants, or changes in the number of individuals present.

The order of decreasing compensatory ability, *M. paniculata*, *A. millefolium* and *F. altaica*, may contribute to relative plant performance during this time, but conditions other than nutrient availability and regrowth must be operating. These could include competition (Lee and Bazazz 1980), seasonal timing of herbivory (Gedge and Maun 1992) and selective herbivore feeding preference (Crawley 1990).

CONCLUSION

From the plants perspective, regrowth ability depends on the species, soil fertility and the growth measure considered. In terms of final leaf area, compensatory ability is the same for all three species in both low and high-nutrient soils. For all biomass variables, the compensatory ability of *F. altaica* was improved with fertilization whereas the compensatory abilities of *M. paniculata* and *A. millefolium* were reduced. From the animal's perspective, compensatory ability was always reduced with fertilization. As the perspective considered affects which model is supported, future studies comparing the impact of defoliation on plant growth under different resource levels should be consider both proportional and absolute data. From the plant's perspective, compensatory ability is best assessed using the proportional size of eaten plants relative to uneaten neighbours in the same soil type. Proportional growth is important to a plant as it may determine the outcome of competition for light and nutrients. Absolute growth measures best assess the impact of leaf loss on animal food supply.

Nutrient supplementation can alter the compensatory responses shown by plants (Maschinski and Whitham 1989, Hik and Jefferies 1990, Hik *et al.* 1991), but responses to naturally occurring levels of soil nutrients are clearly most relevant. Plants at Kluane generally grow in nutrient-poor soils and it was under these conditions that plants were more likely to compensate for tissue loss. These results indicate that current models need to incorporate the natural level of resource availability that plants may be adapted to, prior to a herbivory event. The one exception, *F. altaica*, calls for investigation of the reasons for species differences in regrowth response.

The majority of compensatory studies have been carried out on herbaceous or woody plants in temperate regions (Obeso 1993), which could account for the predictions and support of the CRM. Resources are generally more abundant in temperate zones than in sub-arctic areas such as Kluane, which may explain why two of the three species studied here conformed to the predictions of the GRM. Future studies could compare the regrowth responses of plants native to areas of high or low resource availability to test whether compensatory ability is enhanced under the native soil nutrient conditions. If plants are genetically adapted to a certain resource level, they may better compensate for tissue loss under such conditions.

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Table 1. The growth habits, snowshoe hare eating patterns, and response of the three experimental species to some treatments.

Species	Growth Habit (Hulten 1968)	Consumption by herbivores (Hik pers.comm.)	Response (% cover) to six years of fertilizing & hare exclusion treatments (John and Turkington 1995)
F. altaica	tillering early spring emergence flowers late July through August	stems clipped several cm above ground level stems and leaves eaten	hare exclusion alone had no significant effect for all three species fertilizing increased cover from 20% to 25% fertilizing + hare exclusion increased cover from 20% to 55%
A. millefolium	slender rhizome branching stems 30cm to 60cm in height flowers July through August	entire leaves, or leaf tips, are removed	fertilizing increased cover from 1% to 2% fertilizing + hare exclusion increased cover from 1% to 5%
M. paniculata	clumped growth habit 30 to 70cm in height flowers in July	entire leaves, or leaf tips are removed	fertilizing increased cover from 1% to 5% fertilizing + hare exclusion increased cover from 1% to 12%

Table 2. Sample sizes (reduced from n = 12) for treatment combinations where pre-clipping mortality occurred.

Species	Leaf loss	Short-term fertilization	Long-term fertilization	Sample size
F. altaica	0 %	unfertilized	unfertilized	11
M. paniculata	0%	unfertilized	unfertilized	11
	0%	unfertilized	fertilized	10
	0%	fertilized	fertilized	10
	50%	unfertilized	unfertilized	8
	50%	fertilized	unfertilized	11
	100%	fertilized	fertilized	11

Table 3. Summary of ANOVA for the relative growth rate (RGR) of leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B). Degrees of freedom (df), Fisher's ratio (F-value), Probability (Pr).

Source	df	F-value	Pr > F
B	11	1.67	0.0785
B x FS	11	1.41	0.1675
C	2	835.93	**0.0001**
FS*	1	65.06	**0.0001**
FL	1	0.28	0.5976
S	2	649.06	**0.0001**
C x FS	2	7.35	**0.0008**
C x FL	2	6.54	**0.0016**
C x S	4	434.75	**0.0001**
FS x FL	1	10.86	**0.0011**
FS x S	2	7.75	**0.0005**
FL x S	2	3.19	**0.0425**
C x FS x FL	2	0.07	0.9334
C x FS x S	4	7.81	**0.0001**
C x FL x S	4	3.64	**0.0065**
FS x FL x S	2	5.21	**0.0059**
C x FS x FL x S	4	1.49	0.2036

Note: For bold-typed values, $P < 0.05$.

* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 4. Summary of ANOVA for proportional post-clipping growth of leaf area of clipped plants relative to unclipped controls. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	3.64	**0.0001**
B x FS	11	1.83	**0.0525**
C	1	0.79	0.3752
FS*	1	11.84	**0.0055**
FL	1	39.77	**0.0001**
S	2	0.9	0.4077
C x FS	1	1.31	0.2531
C x FL	1	0.87	0.3511
C x S	2	0.23	0.7972
FS x FL	1	0.001	0.9766
FS x S	2	1.48	0.2312
FL x S	2	1.78	0.1718
C x FS x FL	1	0.28	0.5995
C x FS x S	2	0.46	0.6293
C x FL x S	2	1.89	0.1536
FS x FL x S	2	1.37	0.2578
C x FS x FL x S	2	1.59	0.2065

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 5. Summary of ANOVA for proportional final leaf area of clipped plants relative to unclipped controls. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	1.78	0.0595
B x FS	11	2.06	**0.0248**
C	1	24.96	**0.0001**
FS*	1	1.01	0.3357
FL	1	0.95	0.3311
S	2	0.44	0.6434
C x FS	1	0.06	0.7993
C x FL	1	0.71	0.3998
C x S	2	0.77	0.4626
FS x FL	1	0.43	0.5145
FS x S	2	1.37	0.2576
FL x S	2	0.28	0.7535
C x FS x FL	1	0.47	0.4924
C x FS x S	2	1.74	0.1791
C x FL x S	2	4.68	**0.0103**
FS x FL x S	2	0.13	0.8785
C x FS x FL x S	2	1.61	0.2019

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 6. Summary of ANOVA for proportional above-ground biomass of clipped plants relative to unclipped controls. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	1.65	0.0861
B x FS	11	1.13	0.3372
C	1	25.81	**0.0001**
FS*	1	0.39	0.5474
FL	1	4.25	**0.0405**
S	2	2.94	0.0550
C x FS	1	0.17	0.6831
C x FL	1	1.26	0.2629
C x S	2	1.12	0.3269
FS x FL	1	0.37	0.5445
FS x S	2	6.46	**0.0019**
FL x S	2	0.25	0.7758
C x FS x FL	1	0.01	0.9071
C x FS x S	2	3.22	**0.0421**
C x FL x S	2	0.77	0.4647
FS x FL x S	2	0.50	0.6071
C x FS x FL x S	2	0.14	0.8653

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 7. Summary of ANOVA for proportional below-ground biomass of clipped plants relative to unclipped controls. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	2.21	**0.0153**
B x FS	11	1.39	0.1807
C	1	2.00	0.1586
FS*	1	4.54	0.0564
FL	1	0.62	0.4320
S	2	1.41	0.2455
C x FS	1	1.78	0.1831
C x FL	1	0.02	0.9015
C x S	2	0.63	0.5318
FS x FL	1	0.25	0.6171
FS x S	2	4.46	**0.0127**
FL x S	2	0.65	0.5242
C x FS x FL	1	1.43	0.2329
C x FS x S	2	1.11	0.3366
C x FL x S	2	0.08	0.9195
FS x FL x S	2	2.37	0.0964
C x FS x FL x S	2	0.29	0.7470

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 8. Summary of ANOVA for proportional total biomass of clipped plants relative to unclipped controls. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	1.60	0.1009
B x FS	11	1.21	0.2810
C	1	13.14	**0.0004**
FS*	1	7.14	**0.0217**
FL	1	1.53	0.2176
S	2	1.61	0.2020
C x FS	1	0.42	0.5186
C x FL	1	0.04	0.8407
C x S	2	0.67	0.5127
FS x FL	1	0.27	0.6037
FS x S	2	4.08	**0.0183**
FL x S	2	0.34	0.7142
C x FS x FL	1	0.88	0.3503
C x FS x S	2	1.26	0.2860
C x FL x S	2	0.07	0.9261
FS x FL x S	2	0.83	0.4362
C x FS x FL x S	2	1.02	0.3609

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 9. Summary of ANOVA for the ratio of above-ground biomass to total biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B). Results for arcsine, square-root transformed data are reported.

Source	df	F-value	Pr > F
B	11	1.19	0.2929
B x FS	11	1.48	0.1372
C	2	30.12	**0.0001**
FS*	1	112.65	**0.0001**
FL	1	30.78	**0.0001**
S	2	160.82	**0.0001**
C x FS	2	2.19	0.1134
C x FL	2	0.18	0.8361
C x S	4	0.85	0.4969
FS x FL	1	0.34	0.5579
FS x S	2	0.69	0.5025
FL x S	2	9.57	**0.0001**
C x FS x FL	2	0.25	0.7763
C x FS x S	4	0.3	0.8765
C x FL x S	4	1.64	0.1631
FS x FL x S	2	0.36	0.6972
C x FS x FL x S	4	2.00	0.0946

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 10. Summary of ANOVA for absolute post-clipping growth of leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	3.27	**0.0003**
B x FS	11	1.34	0.2023
C	2	4.22	**0.0155**
FS*	1	91.04	**0.0001**
FL	1	11.15	**0.0009**
S	2	63.89	**0.0001**
C x FS	2	9.97	**0.0001**
C x FL	2	0.19	0.8294
C x S	4	0.25	0.9114
FS x FL	1	1.16	0.2823
FS x S	2	21.61	**0.0001**
FL x S	2	10.68	**0.0001**
C x FS x FL	2	0.36	0.6972
C x FS x S	4	1.34	0.2537
C x FL x S	4	0.19	0.9439
FS x FL x S	2	1.41	0.2444
C x FS x FL x S	4	0.21	0.9338

Note: For bold-typed values, P < 0.05.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 11a. Summary of ANOVA for absolute final leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	3.52	**0.0001**
B x FS	11	1.05	0.4037
C	2	22.37	**0.0001**
FS*	1	90.82	**0.0001**
FL	1	13.06	**0.0003**
S	2	79.96	**0.0001**
C x FS	2	8.2	**0.0003**
C x FL	2	0.35	0.7030
C x S	4	3.07	**0.0166**
FS x FL	1	1.39	0.2392
FS x S	2	18.06	**0.0001**
FL x S	2	8.95	**0.0002**
C x FS x FL	2	0.52	0.5973
C x FS x S	4	1.24	0.2948
C x FL x S	4	0.21	0.9306
FS x FL x S	2	0.83	0.4379
C x FS x FL x S	4	0.18	0.9497

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 11b. Absolute change in final leaf area of 100%-clipped plants relative to unclipped controls at the end of the experiment, for the three species at the two levels of short-term fertilization. Negative signs (-) indicate a reduction in final leaf area.

Short-term fertilization	Species	Leaf area (cm^2)
unfertilized	*A. millefolium*	- 6.3
	F. altaica	- 74.4
	M. paniculata	- 3.6
fertilized	*A. millefolium*	- 40.5
	F. altaica	- 150.4
	M. paniculata	- 152.8

Table 12a. Summary of ANOVA for absolute above-ground biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	3.94	**0.0001**
B x FS	11	2.33	**0.0089**
C	2	56.47	**0.0001**
FS*	1	59.06	**0.0001**
FL	1	39.77	**0.0001**
S	2	1.39	0.2492
C x FS	2	13.48	**0.0001**
C x FL	2	3.02	**0.0499**
C x S	4	1.88	0.1133
FS xFL	1	7.19	**0.0077**
FS x S	2	2.32	0.1000
FL x S	2	5.72	**0.0036**
C x FS x FL	2	1.09	0.338
C x FS x S	4	2.02	0.0916
C x FL x S	4	1.28	0.2769
FS x FL x S	2	2.49	0.0844
C x FS x FL x S	4	0.80	0.5289

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 12b. Absolute change in above-ground biomass at the end of the experiment for 100%-clipped plants relative to unclipped controls at two levels of short-term fertilization and two levels of long-term fertilization. Positive signs (+) indicate an increase in above-ground biomass.

Fertilization		Biomass (g)
short-term	unfertilized	+ 0.45
	fertilized	+ 1.105
long-term	unfertilized	+ 0.595
	fertilized	+ 0.961

Table 13a. Absolute changes in below-ground biomass at the end of the experiment of 50%-clipped plants relative to unclipped controls at eight long-term fertilization, short-term fertilization and species combinations.

Long-term fertilization	Short-term fertilization	Species	Biomass (g)
unfertilized	unfertilized	*A. millefolium, M. paniculata*	+ 0.024
		F. altaica	-0.403
	fertilized	*A. millefolium, M. paniculata*	-0.125
		F. altaica	+ 0.109
fertilized	unfertilized	*A. millefolium, M. paniculata*	+ 0.031
		F. altaica	+ 0.61
	fertilized	*A. millefolium, M. paniculata*	-0.101
		F. altaica	-0.573

Table 13b. Summary of ANOVA for absolute below-ground biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	1.13	0.3396
B x FS	11	0.86	0.5801
C	2	4.49	**0.0119**
FS*	1	1.52	0.2433
FL	1	3.93	**0.0481**
S	2	115.33	**0.0001**
C x FS	2	1.48	0.2285
C x FL	2	0.18	0.8394
C x S	4	1.28	0.2783
FS x FL	1	2.49	0.1153
FS x S	2	4.83	**0.0085**
FL x S	2	2.62	0.0744
C x FS x FL	2	2.26	0.1054
C x FS x S	4	0.47	0.7546
C x FL x S	4	0.18	0.9496
FS x FL x S	2	1.84	0.1599
C x FS x FL x S	4	2.59	**0.0366**

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 14. Summary of ANOVA for absolute total biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B).

Source	df	F-value	Pr > F
B	11	2.3	**0.0099**
B x FS	11	0.99	0.4575
C	2	22.96	**0.0001**
FS*	1	16.05	**0.0021**
FL	1	17.98	**0.0001**
S	2	84.13	**0.0001**
C x FS	2	4.18	**0.0161**
C x FL	2	0.57	0.5679
C x S	4	1.95	0.1015
FS x FL	1	0.02	0.8761
FS x S	2	5.61	**0.0040**
FL x S	2	0.1	0.9086
C x FS x FL	2	2.52	0.0818
C x FS x S	4	0.37	0.8279
C x FL x S	4	0.53	0.7121
FS x FL x S	2	3.04	**0.0489**
C x FS x FL x S	4	0.9	0.4617

Note: For bold-typed values, P < 0.05.

* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 15. Summary of ANOVA for vegetative reproduction per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B). Results for log-transformed data are reported.

Source	df	F-value	Pr > F
B	11	3.67	**0.0001**
B x FS	11	2.38	**0.0076**
C	2	12.98	**0.0001**
FS*	1	39.07	**0.0001**
FL	1	19.23	**0.0001**
S	2	67.65	**0.0001**
C x FS	2	2.28	0.1038
C x FL	2	2.63	0.0733
C x S	4	2.87	**0.0232**
FS x FL	1	4.69	**0.0309**
FS x S	2	20.96	**0.0001**
FL x S	2	5.2	**0.0060**
C x FS x FL	2	0.05	0.9536
C x FS x S	4	0.91	0.4567
C x FL x S	4	1.28	0.2755
FS x FL x S	2	0.27	0.7602
C x FS x FL x S	4	1.11	0.3513

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

Table 16. Summary of ANOVA for the ratio of ramet leaf area per plant : total leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS), clipping (C), and block effect (B). Results for arcsine, square-root transformed data are reported.

Source	df	F-value	Pr > F
B	11	2.2	**0.0176**
B x FS	11	0.76	0.6766
C	1	11.15	**0.0011**
FS*	1	0.73	0.4104
FL	1	24.66	**0.0001**
S	1	33.41	**0.0001**
C x FS	1	2.16	0.1437
C x FL	1	0.83	0.3653
C x S	1	0.01	0.9184
FS x FL	1	0.68	0.4109
FS x S	1	1.82	0.1798
FL x S	1	13.26	**0.0004**
C x FS x FL	1	1.65	0.2012
C x FS x S	1	0.00	0.9915
C x FL x S	1	0.98	0.3251
FS x FL x S	1	0.25	0.62
C x FS x FL x S	1	0.06	0.8052

Note: For bold-typed values, $P < 0.05$.
* Due to restrictions in randomization imposed by the split-plot design, tests of hypotheses for the short-term fertilization treatment use the mean square for B x FS as an error term.

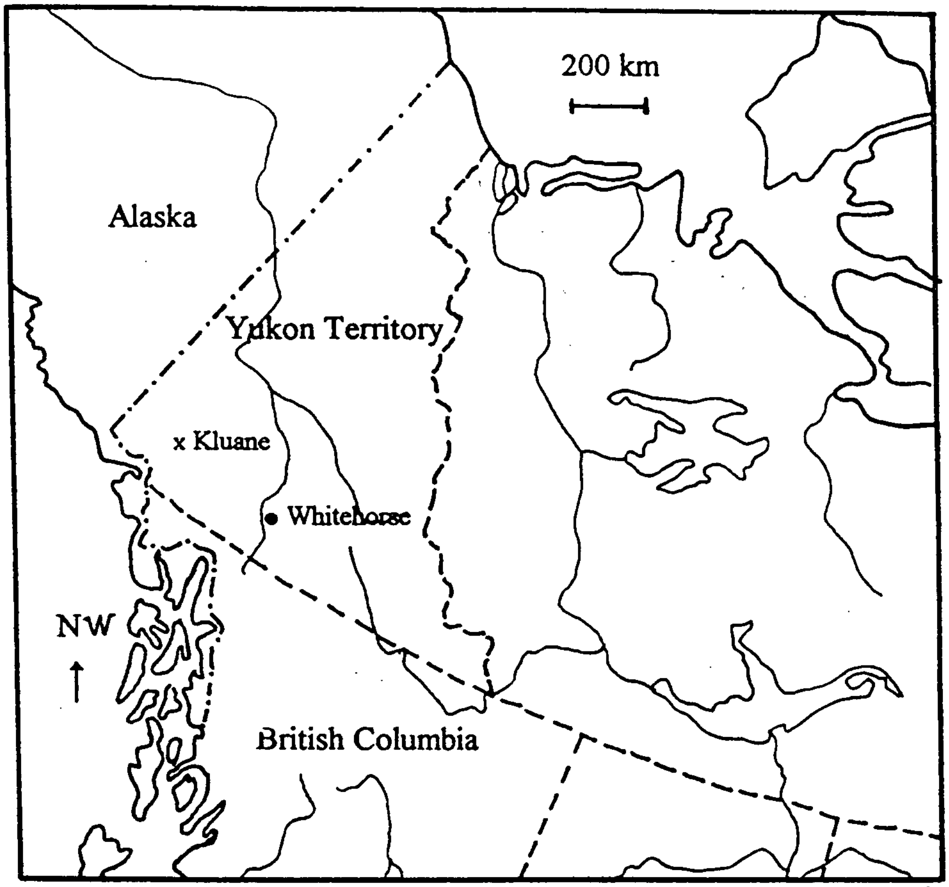


Figure 1. Map of north-western North America showing the location of the study site (x).

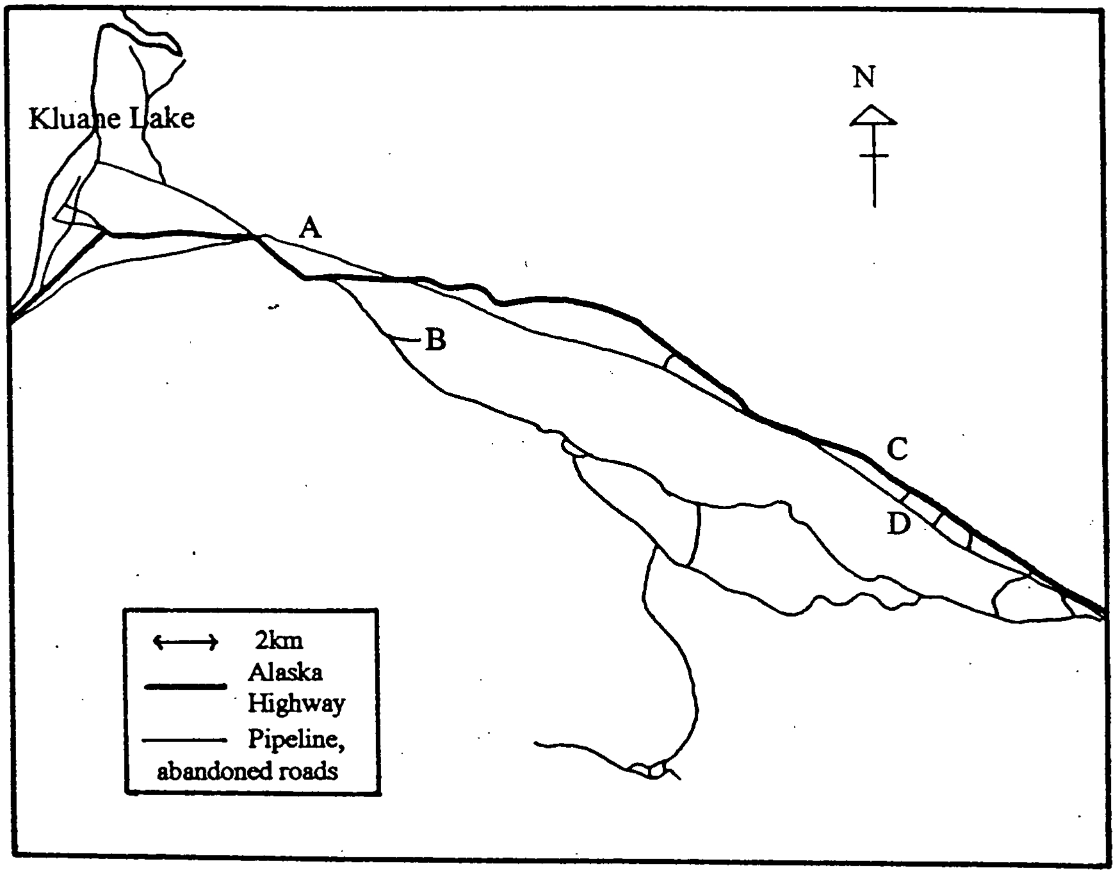


Figure 2. Location of the four transplant collection sites along the Alaska Highway. Site A had a history of long-term fertilization. Sites B, C and D were sites of low-nutrient soils. Site B is also the transplanting site and the location of the microwave tower.

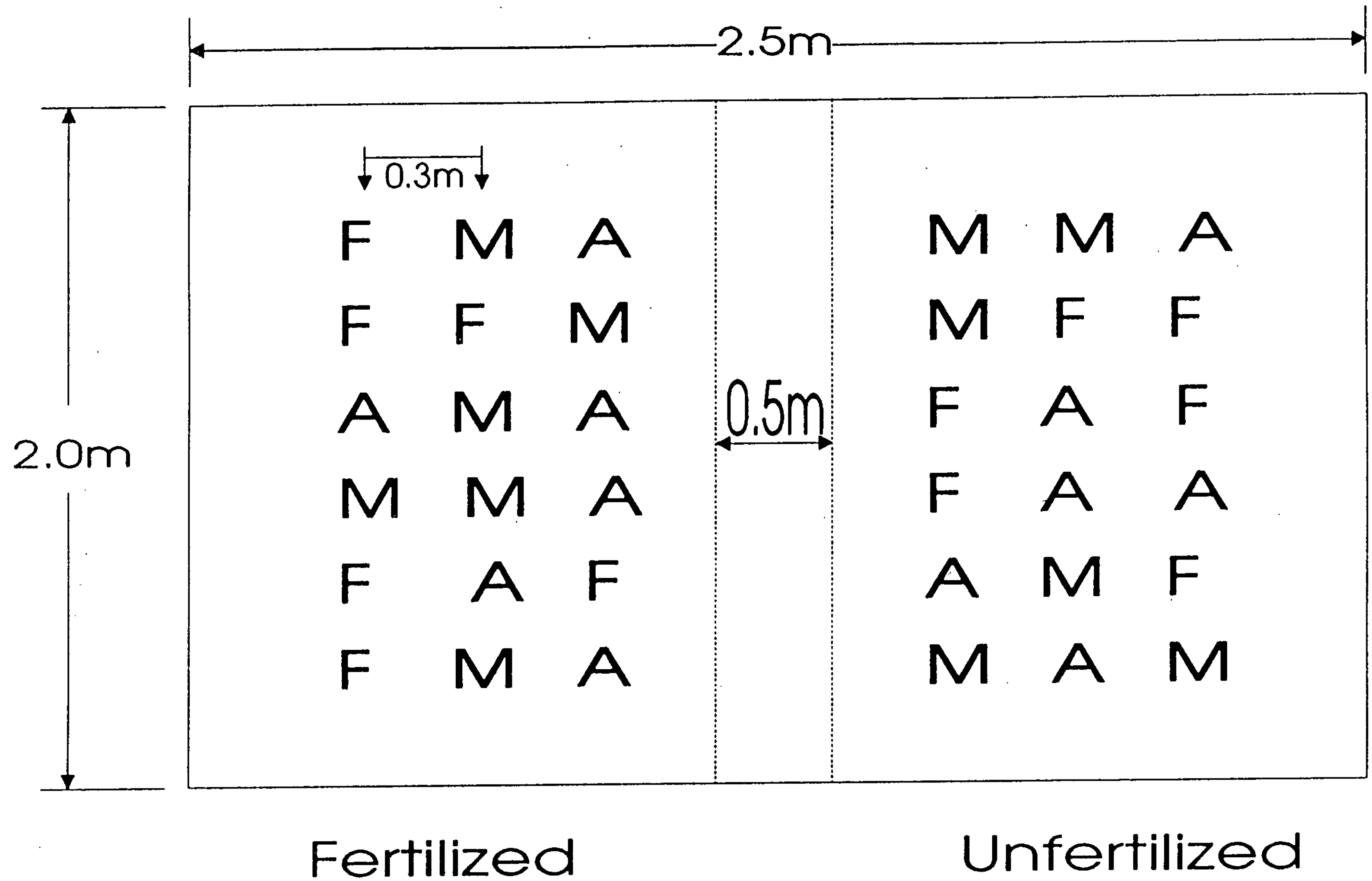
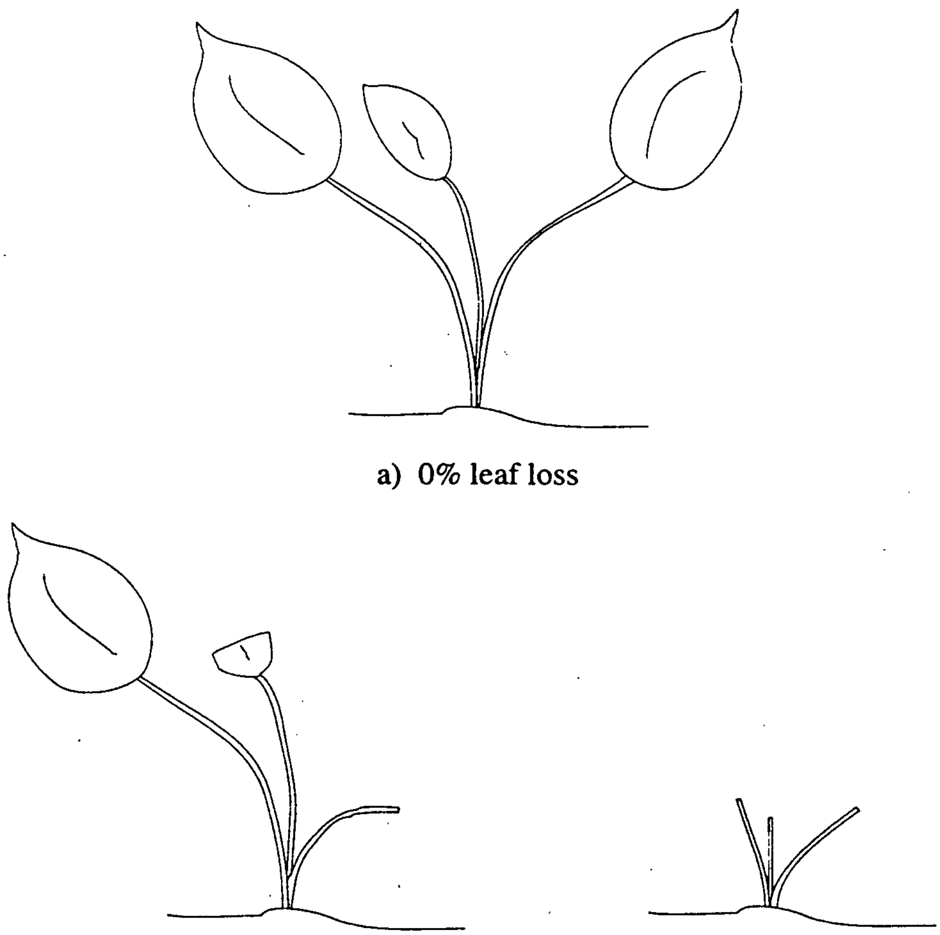


Figure 3. Diagrammatic representation of an experimental plot. The letters A, F and M represent *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata* respectively.



a) 0% leaf loss

b) 50% leaf loss

c) 100% leaf loss

Figure 4. Diagram of the clipping technique used for a) 0%, b) 50%, and c) 100% leaf loss, for *Mertensia paniculata.*

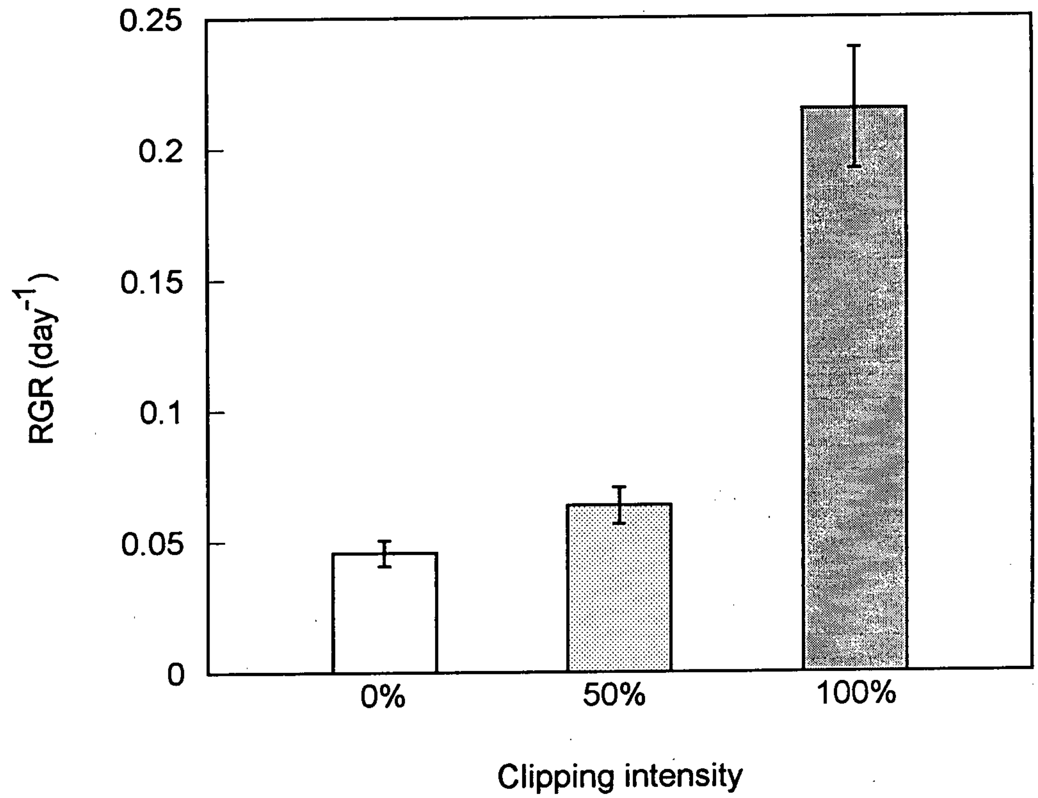


Figure 5. Mean (+/- 1 SE) relative growth rate (RGR) of leaf area, in the first 22 days after clipping, for all species at three intensities of clipping (0% leaf loss, 50% leaf loss and 100% leaf loss).

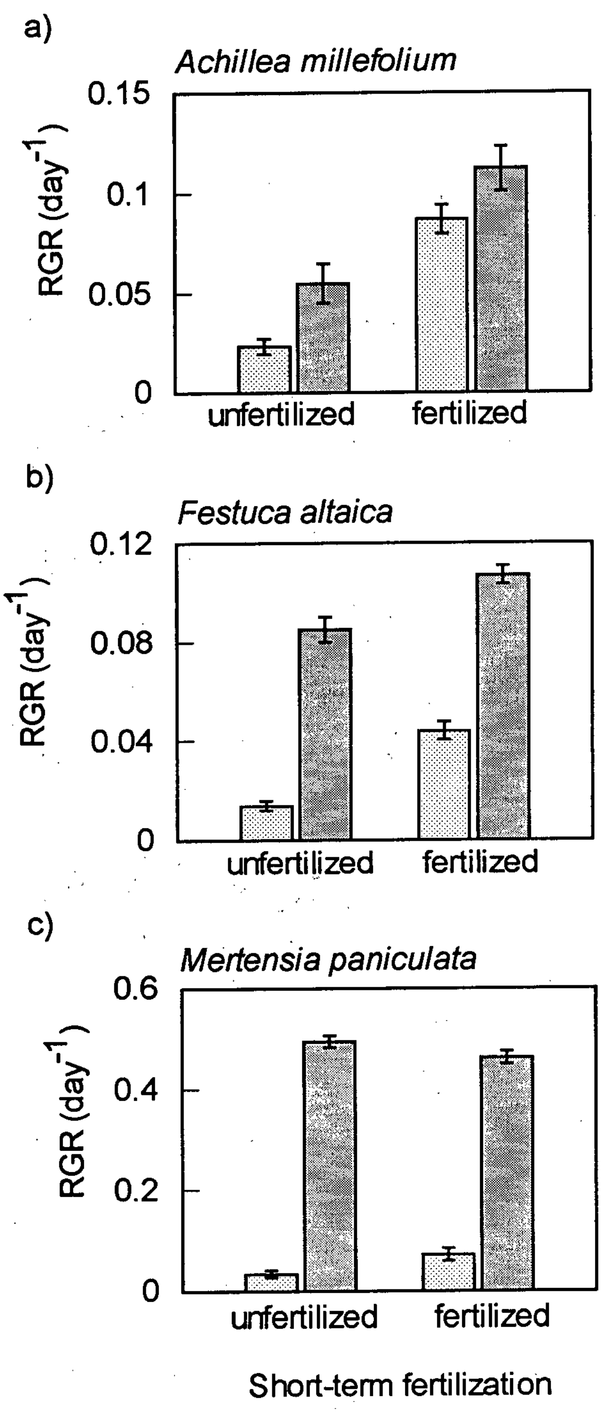


Figure 6. Mean (+/- 1 SE) relative growth rates (RGR) of leaf area of 100%-clipped (▩) and unclipped (▢) plants in the first 22 days after clipping, at two levels of short-term fertilization (unfertilized, fertilized).

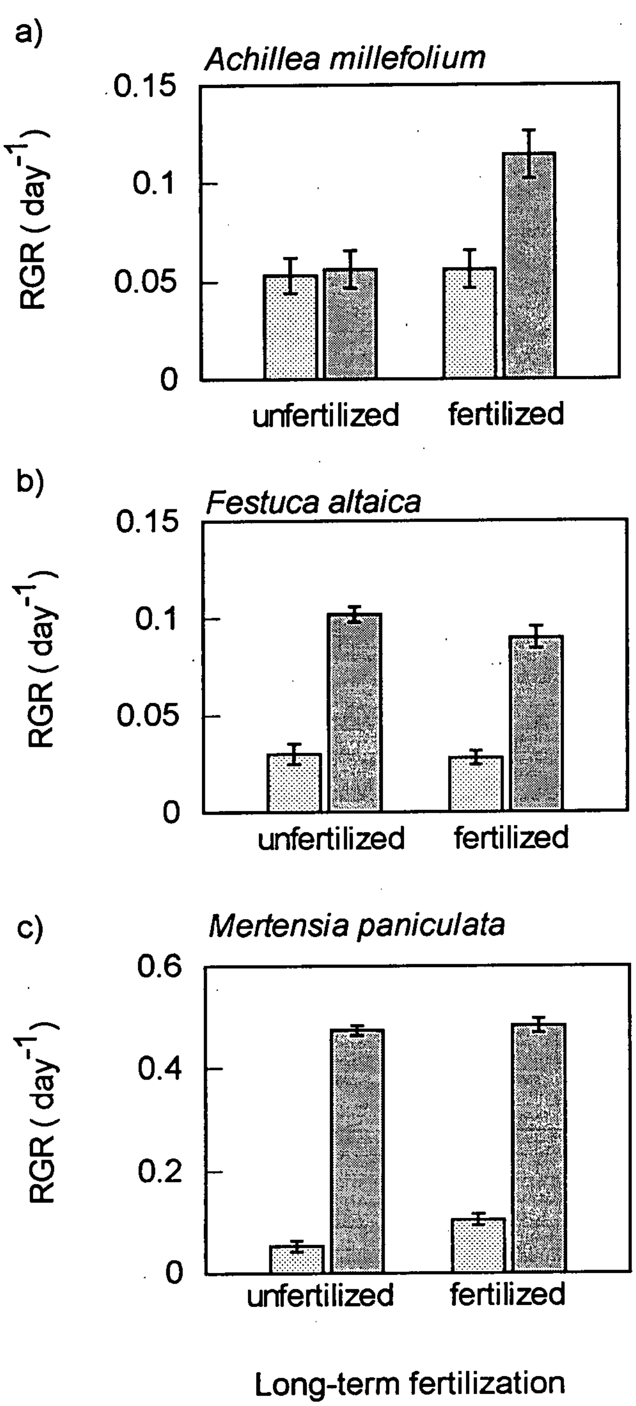


Figure 7. Mean (+/- 1 SE) relative growth rates (RGR) of leaf area of 100%-clipped (▩) and unclipped (▩) plants, in the first 22 days after clipping, at two levels of long-term fertilization (unfertilized and fertilized).

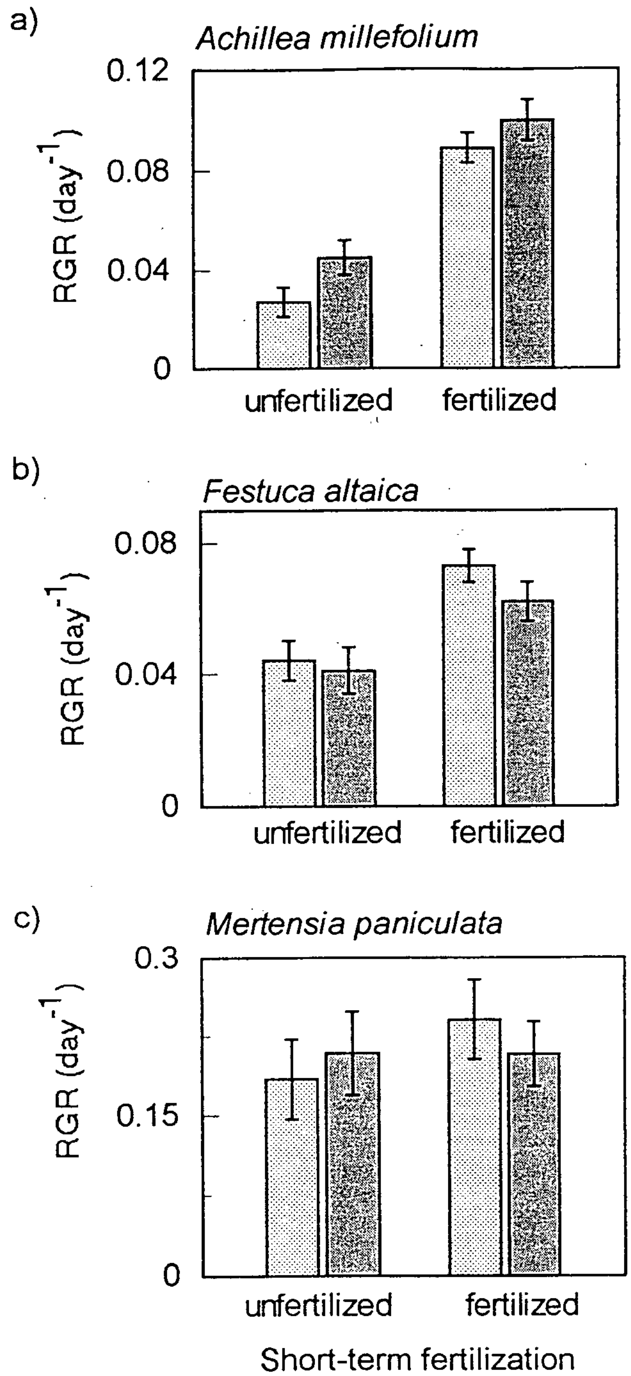


Figure 8. Mean (+/- 1 SE) relative growth rates (RGR) of leaf area of long-term fertilized (▩) and unfertilized (□) plants, in the first 22 days after 100%-clipping, at two levels of short-term fertilization (unfertilized and fertilized).

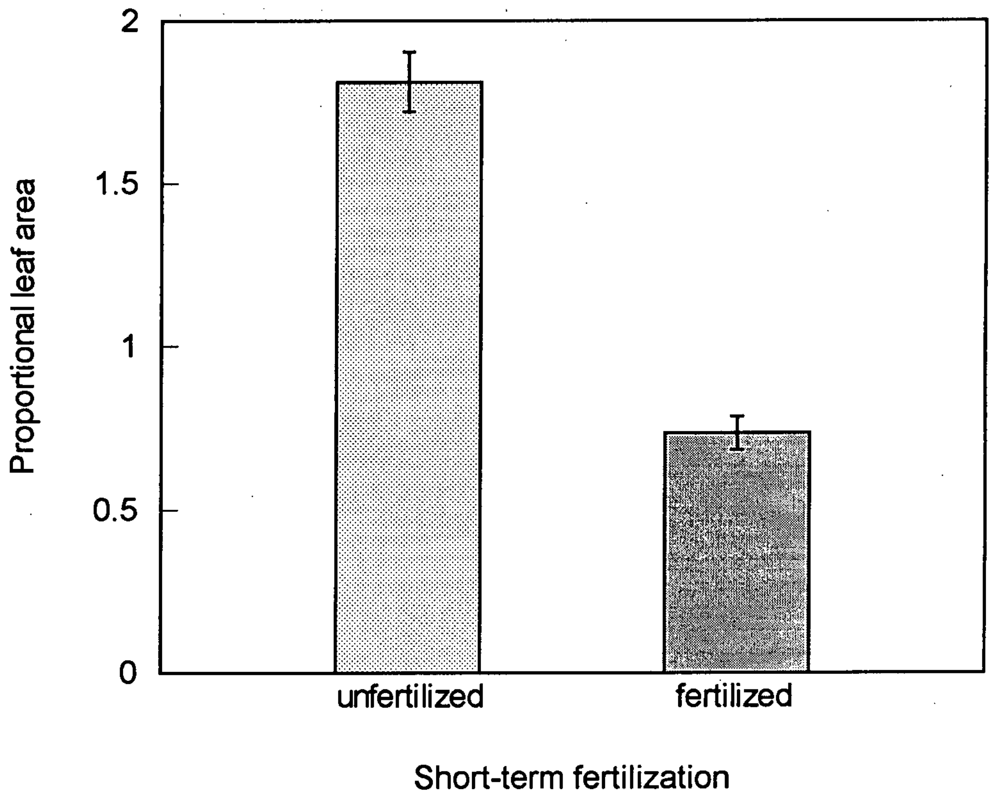


Figure 9. Mean (+/- 1 SE) proportion of leaf area regrowth per plant, 45 days after clipping, for all clipped plants relative to unclipped controls. Data presented are for all species, at two levels of short-term fertilization.

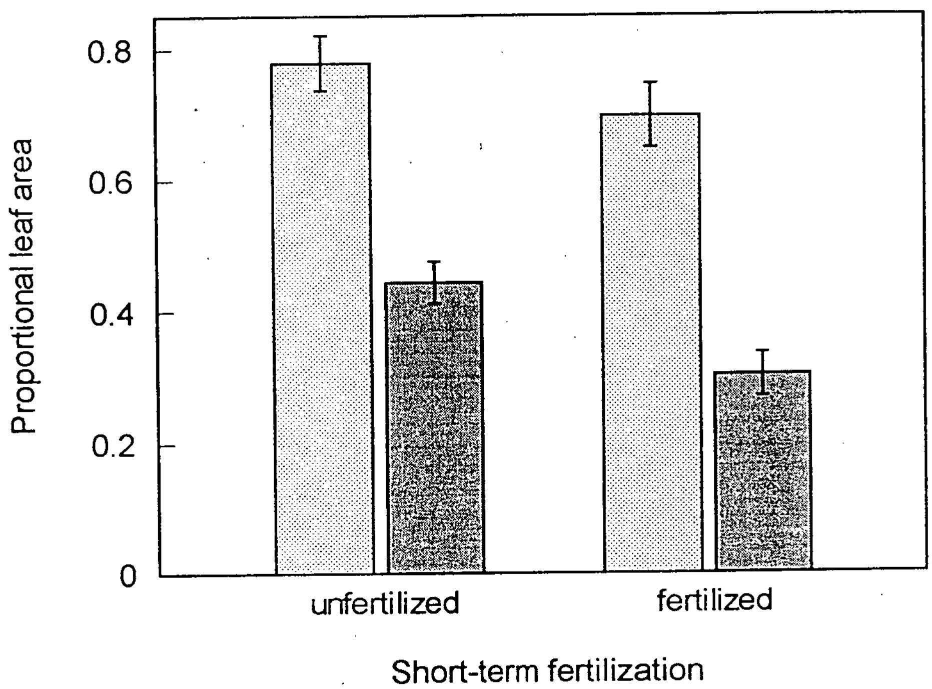


Figure 10. Mean (+/- 1 SE) proportion of final leaf area per plant, 75 days after transplanting, for 50%-clipped ( ) and 100%-clipped ( ) plants, relative to unclipped controls. Data presented are for all species, at two levels of short-term fertilization.

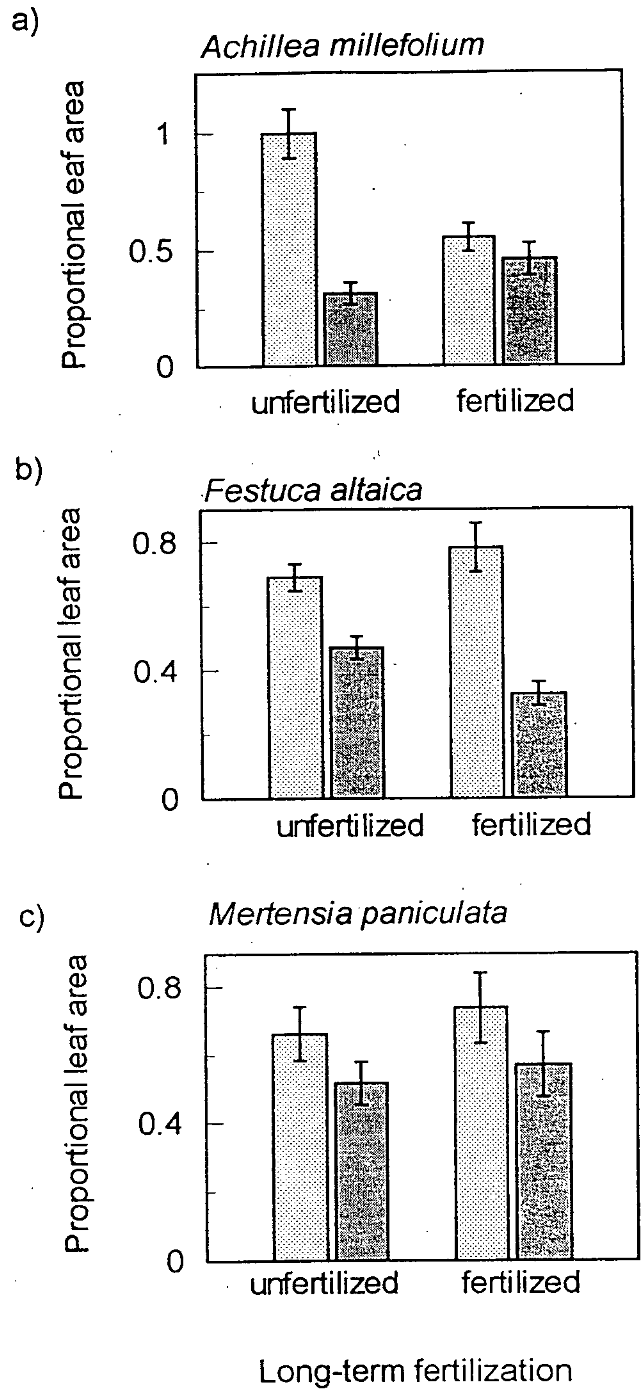


Figure 11. Mean (+/- 1 SE) proportion of final leaf area per plant, 75 days after transplanting, for 50%-clipped ( ) and 100%-clipped ( ) plants, relative to unclipped controls. Data presented are for all species, at two levels of long-term fertilization.

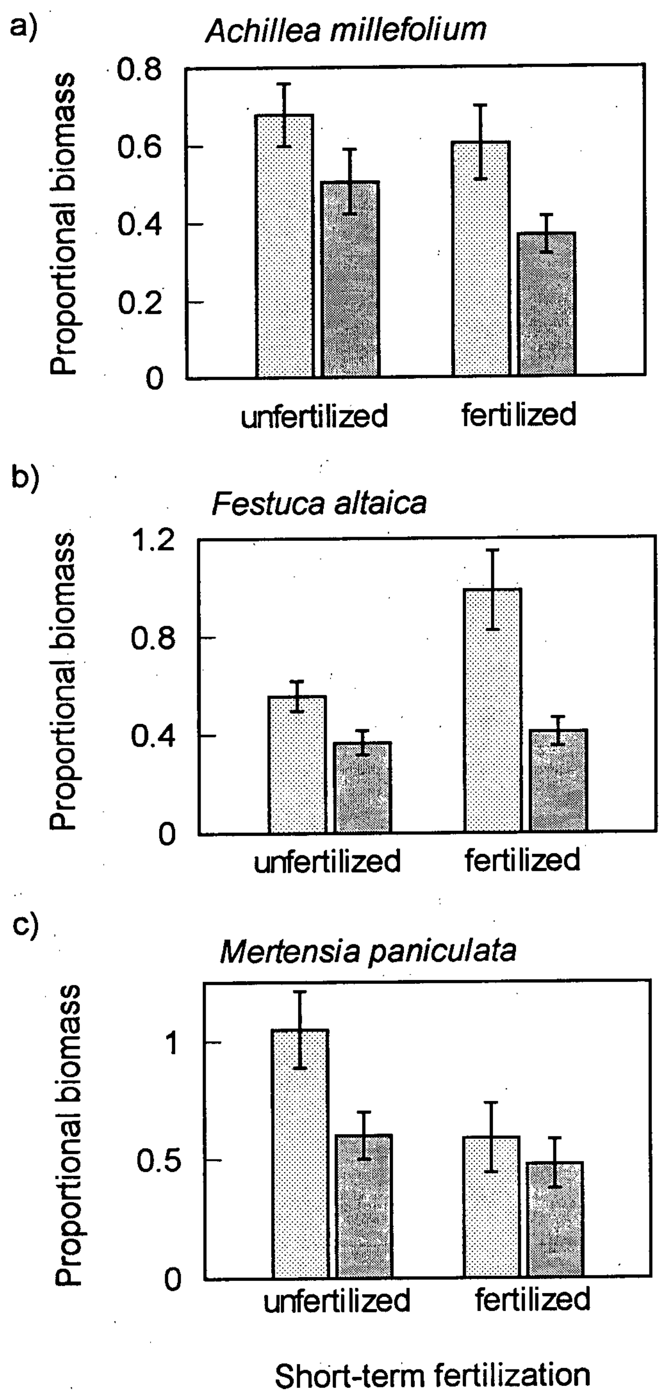


Figure 12. Mean (+/- 1 SE) proportion of above-ground biomass per plant, 75 days after transplanting for 50%-clipped ( ) and 100%-clipped ( ) plants, relative to unclipped controls, at two levels of short-term fertilization.

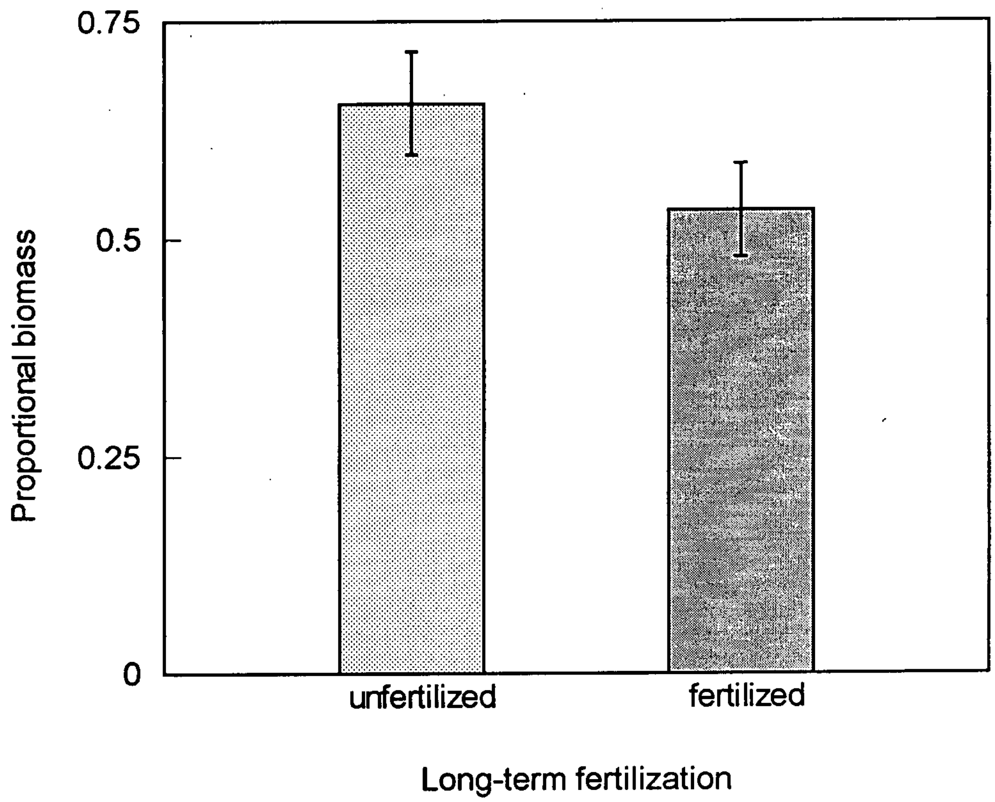


Figure 13. Mean (+/- 1 SE) proportion of above-ground biomass per plant, 75 days after transplanting, of all clipped plants relative to unclipped controls. Data presented are for all species, at two levels of long-term fertilization.

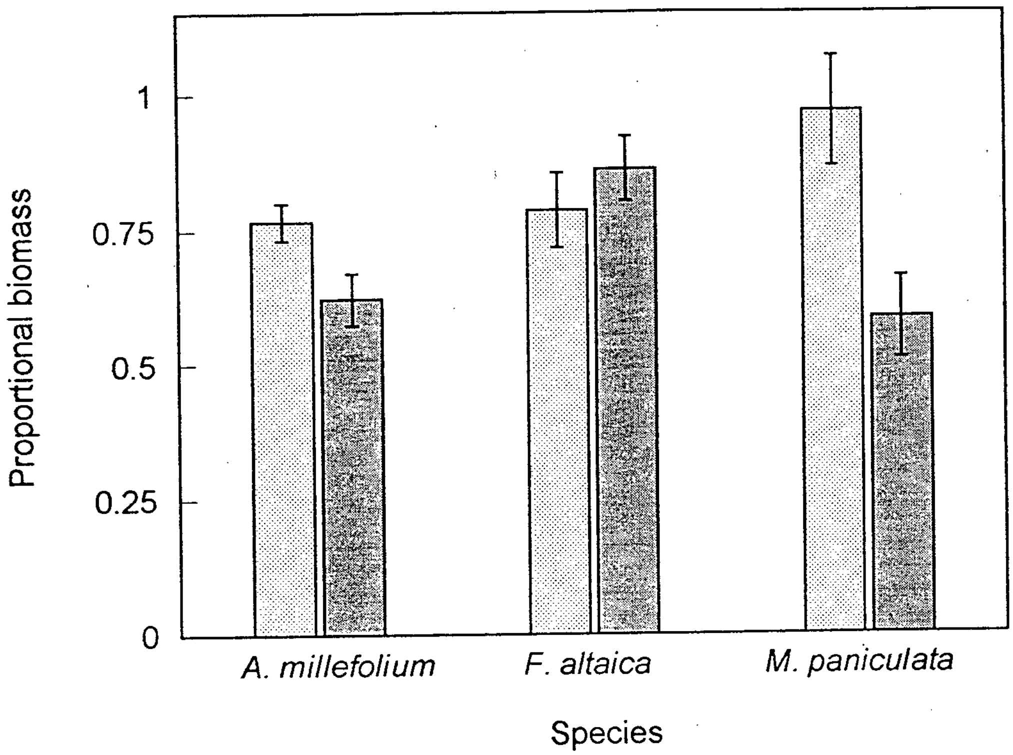


Figure 14. Mean (+/- 1 SE) proportion of below-ground biomass per plant, of clipped plants relative to unclipped controls. Data are presented for *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*, at two levels of short-term fertilization (unfertilized (▢) and fertilized (▦)).

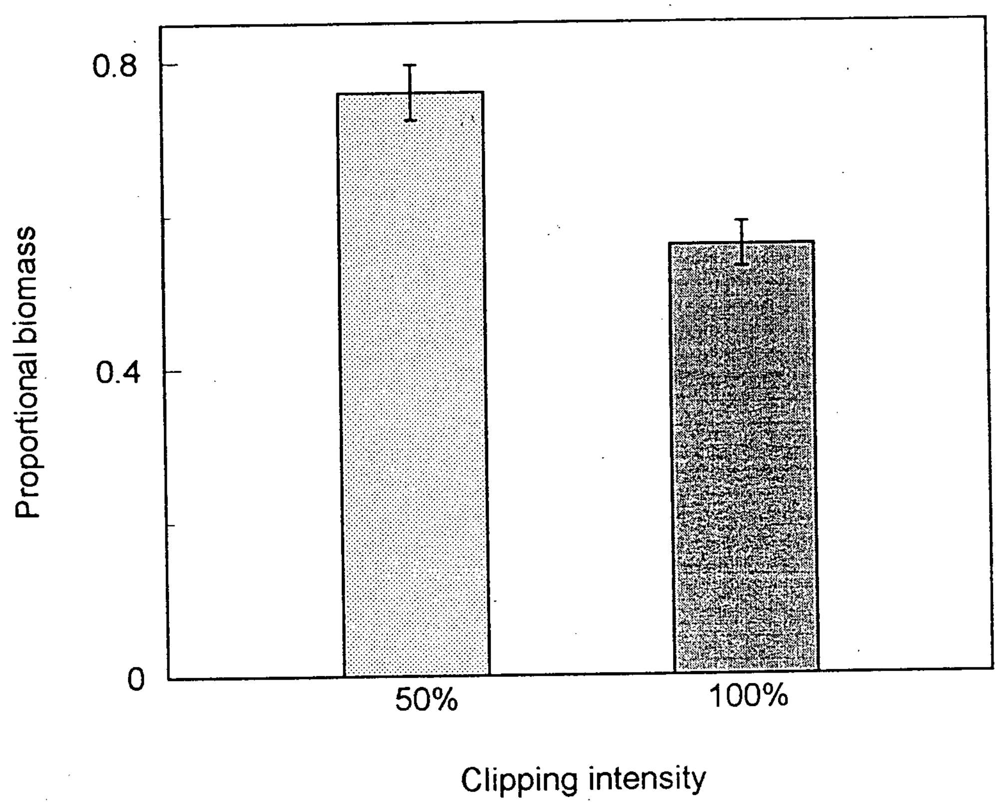


Figure 15. Mean (+/- 1 SE) proportion of total biomass per plant, of 50%-clipped and 100%-clipped plants, relative to unclipped controls, 75 days after transplanting.

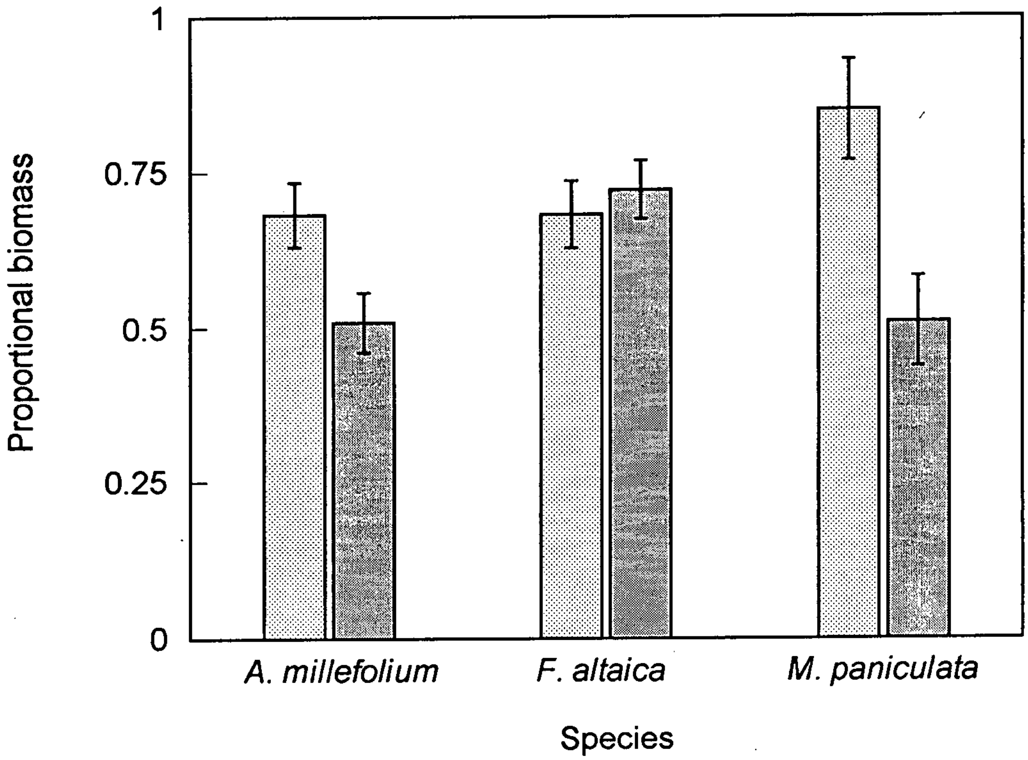


Figure 16. Mean (+/- 1 SE) proportion of total biomass per plant, of clipped plants relative to unclipped controls, for *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata,* at two levels of short-term fertilization (unfertilized (▤) and fertilized (▤)).

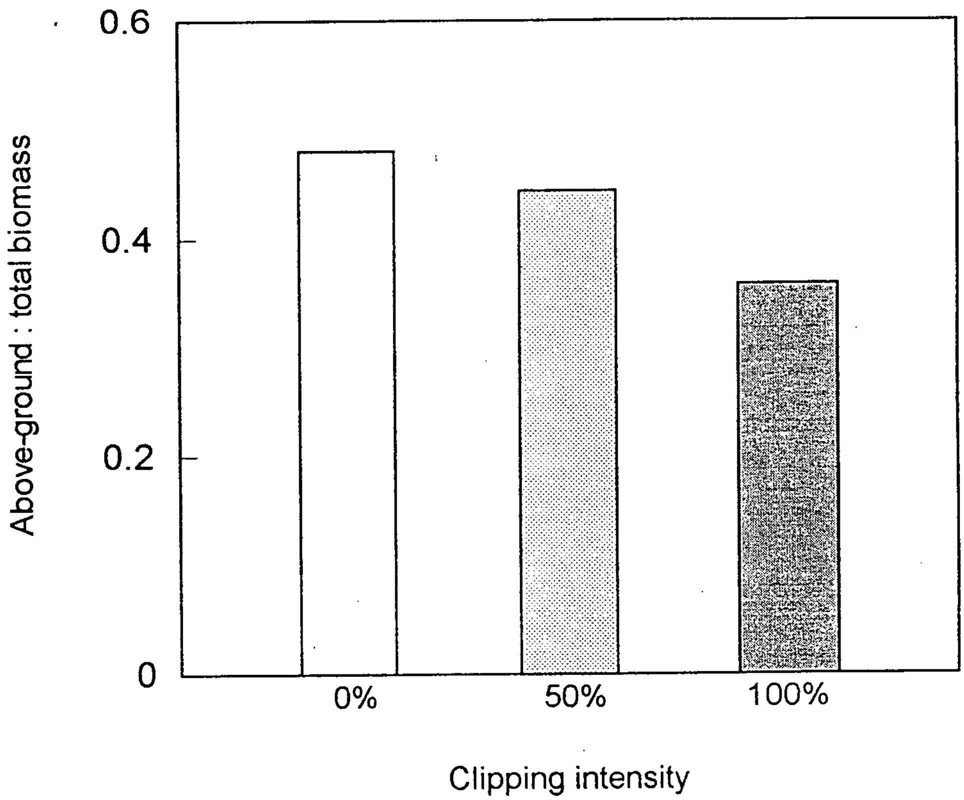


Figure 17. Mean ratio of above-ground biomass : total biomass, per plant, of all species following three intensities of clipping (0%, 50% and 100% leaf loss).

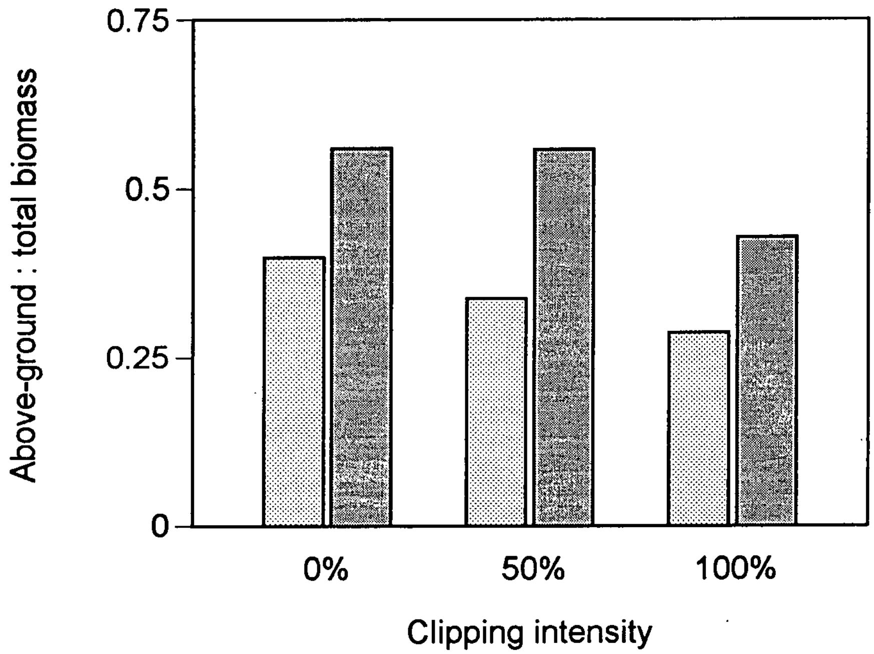


Figure 18. Mean ratio of above-ground biomass : total biomass, per plant, of short-term fertilized ( ) and unfertilized ( ) plants of all species, at three intensities of clipping.

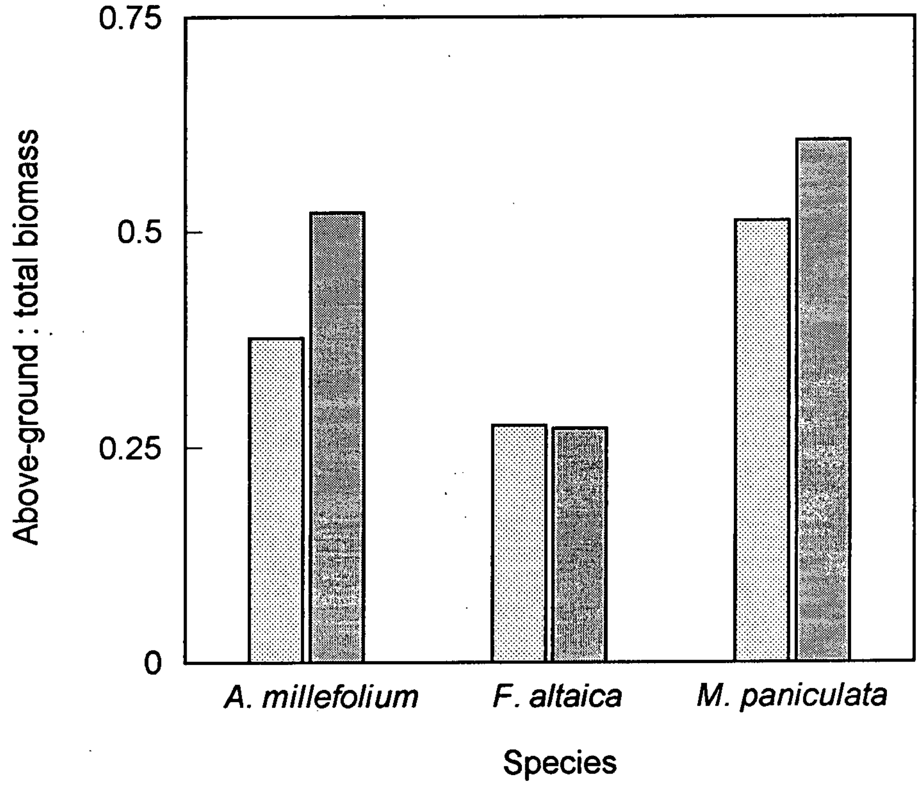


Figure 19. Mean ratio of above-ground biomass : total biomass, per plant, for long-term fertilized (▩) and unfertilized plants (▨) of *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*.

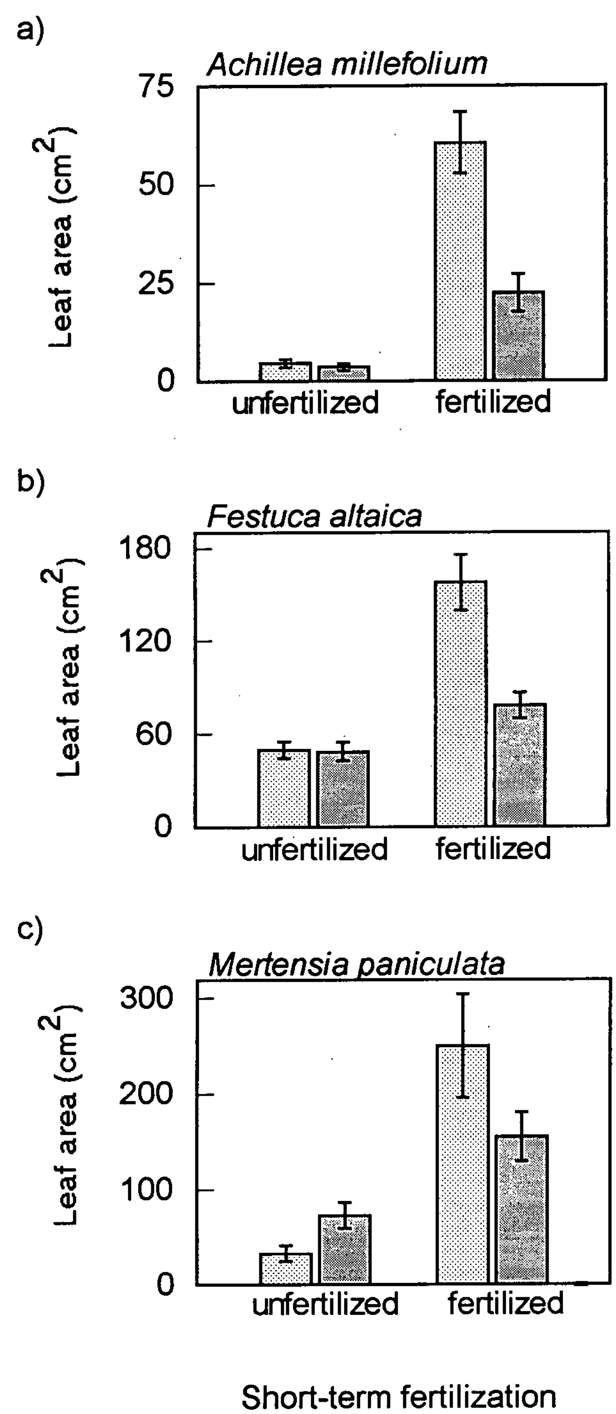


Figure 20. Mean (+/- 1 SE) post-clipping growth of leaf area per plant, in the 45 days after clipping for 100%-clipped ( ) and unclipped ( ) plants of all species, at two levels of short-term fertilization (unfertilized and fertilized).

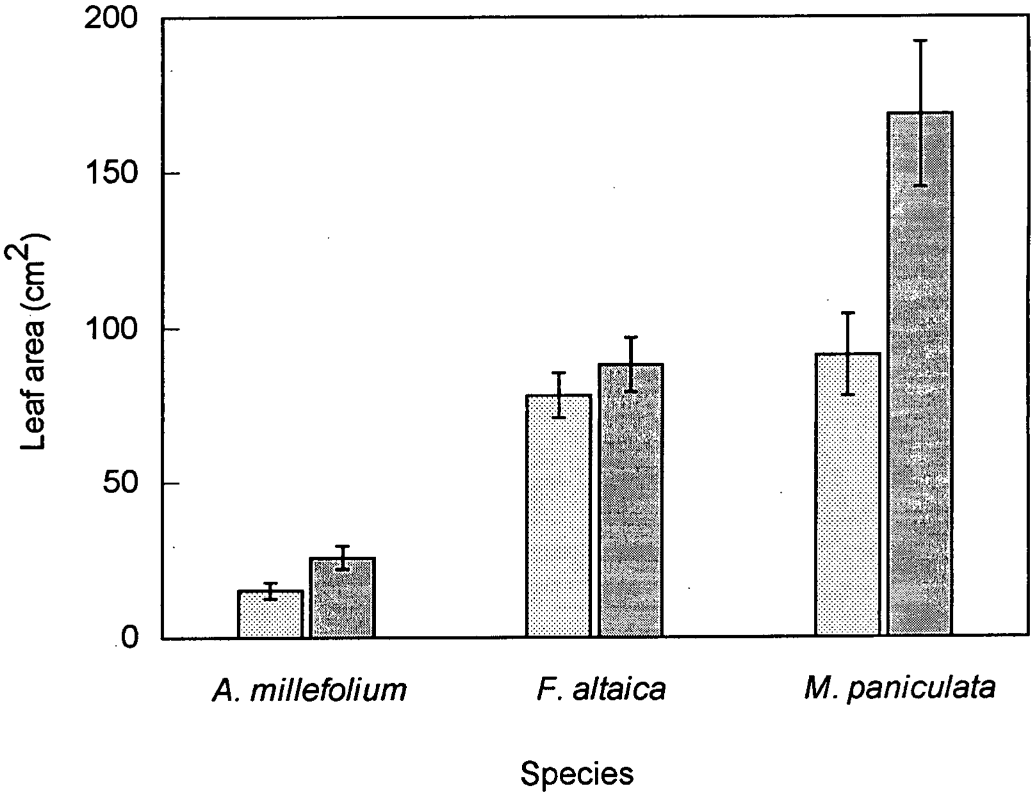


Figure 21. Mean (+/- 1 SE) post-clipping growth of leaf area per plant, in the 45 days following clipping, for long-term fertilized (▩) and unfertilized (▢) plants of *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*.

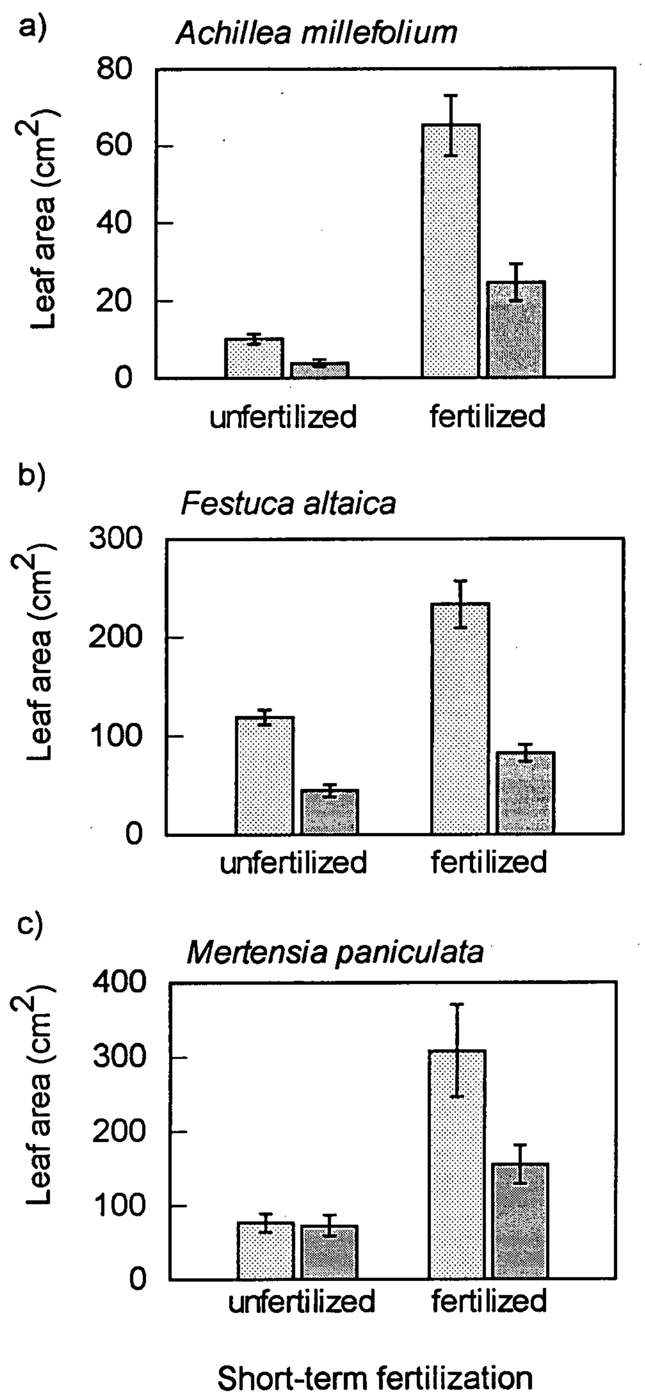


Figure 22. Mean (+/- 1 SE) leaf area per plant, 75 days after transplanting, for 100%-clipped (▩) and unclipped (▨) plants, at two levels of short-term fertilization.

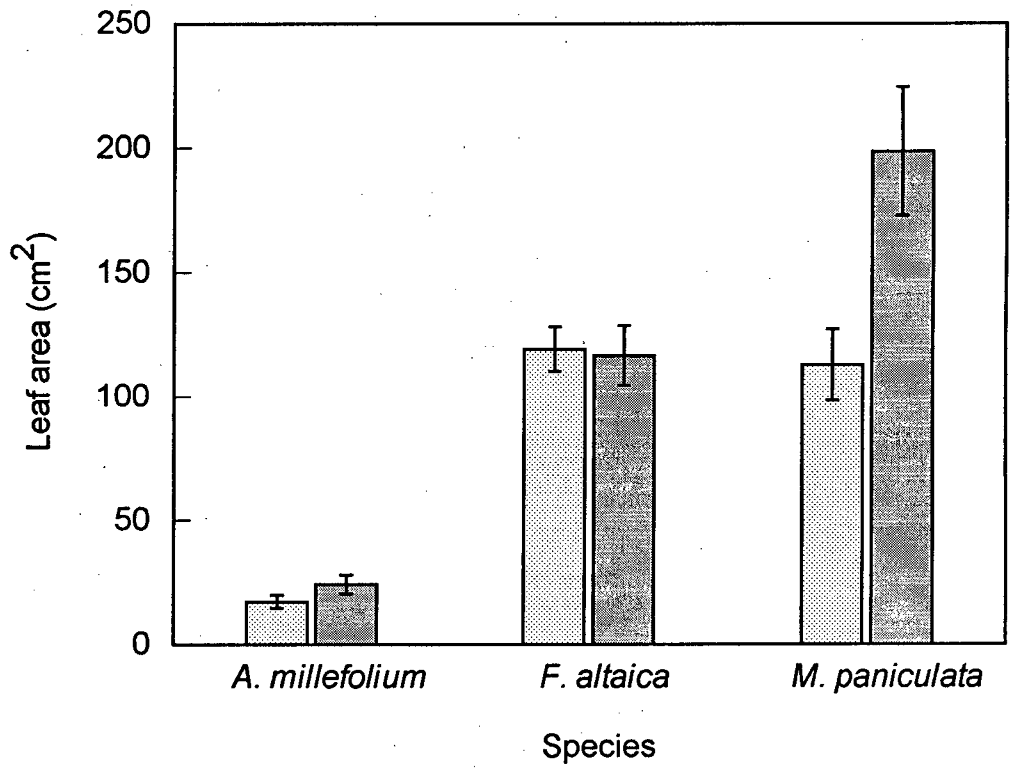


Figure 23. Mean (+/- 1 SE) final leaf area per plant, 75 days after transplanting of long-term fertilized (▦) and unfertilized (▢) plants of *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*.

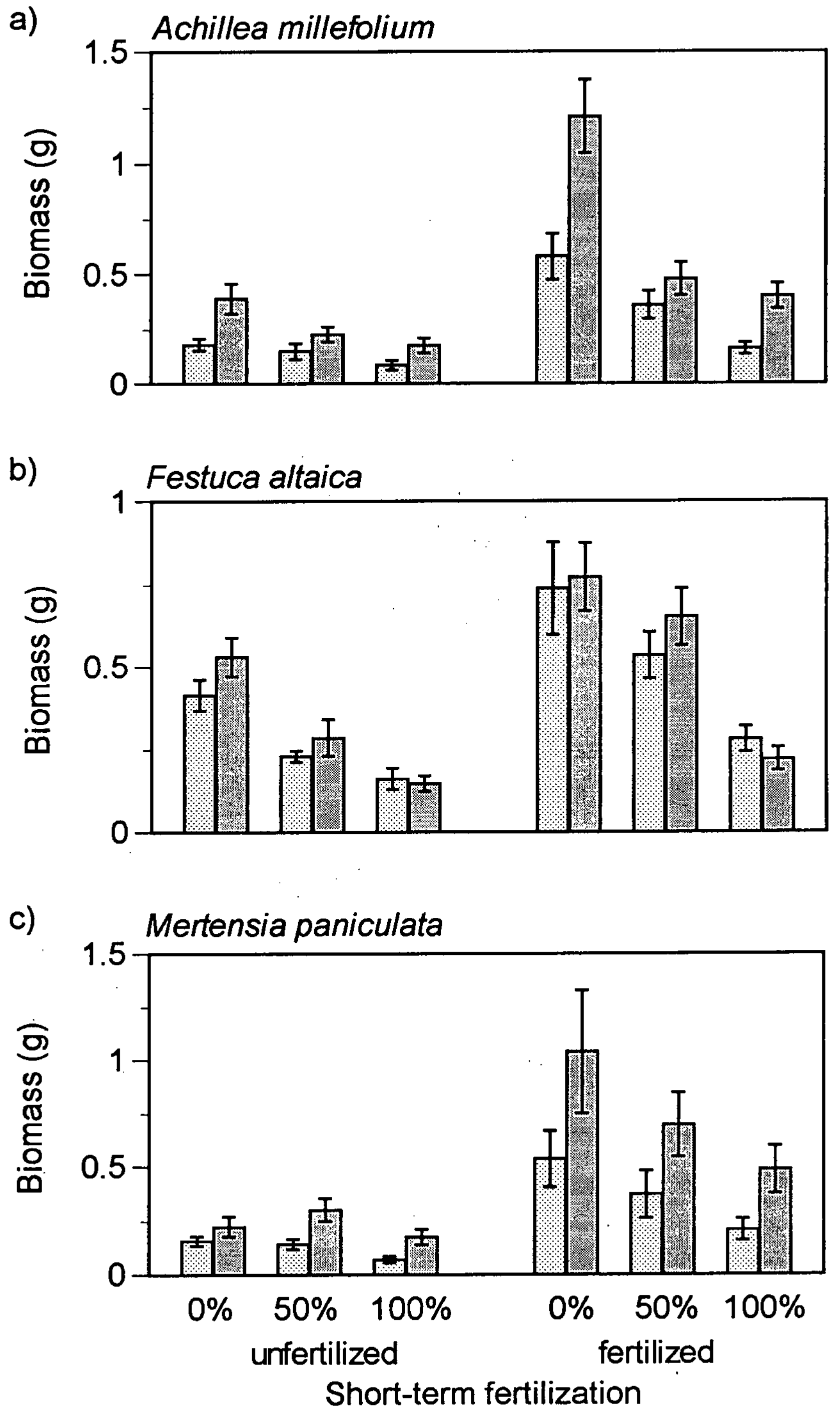


Figure 24. Mean (+/- SE) above-ground biomass per plant, 75 days after transplanting, of long-term fertilized (▩) and unfertilized (▢) plants for three species, at three intensities of clipping (0%, 50% and 100% leaf loss) and two levels of short-term fertilization.

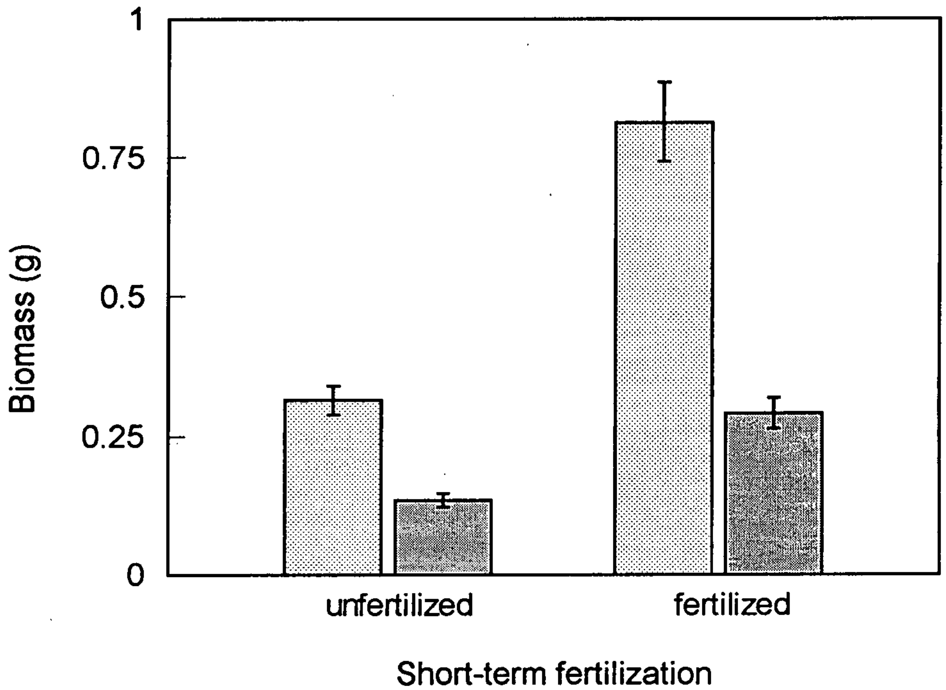


Figure 25. Mean (+/- 1 SE) above-ground biomass per plant, 75 days after transplanting, for 100%-clipped (▩) and unclipped (▨) plants of all species, at two levels of short-term fertilization.

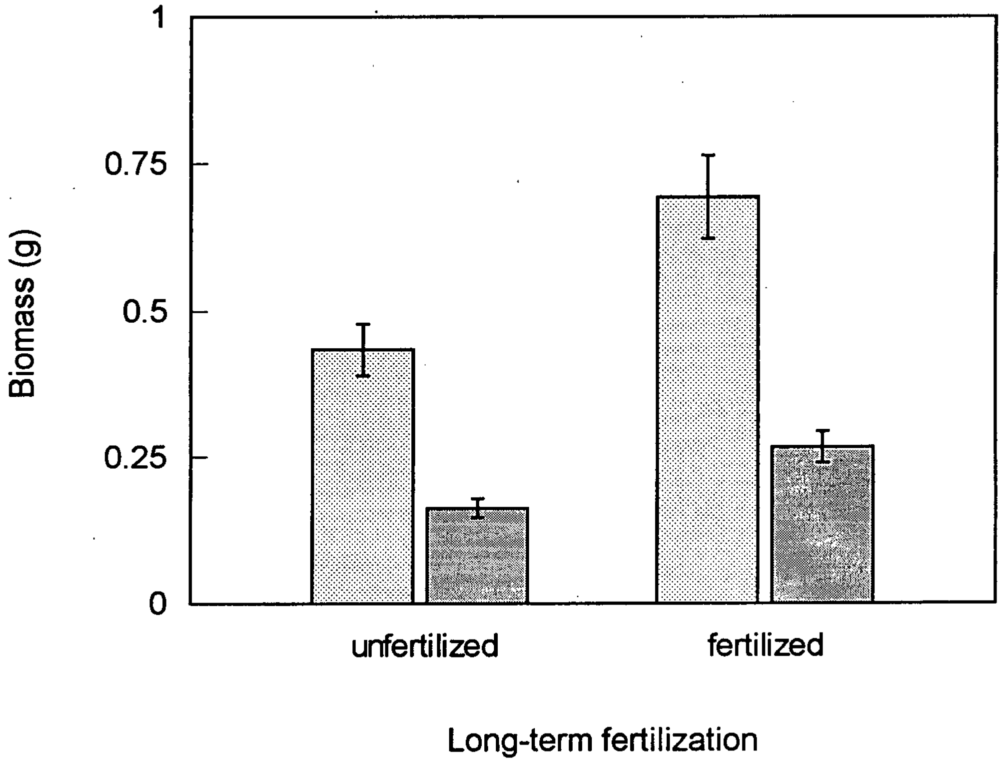


Figure 26. Mean (+/- 1 SE) above-ground biomass per plant, 75 days after transplanting, for 100%-clipped ( ) and unclipped ( ) plants of all species, at two levels of long-term fertilization.

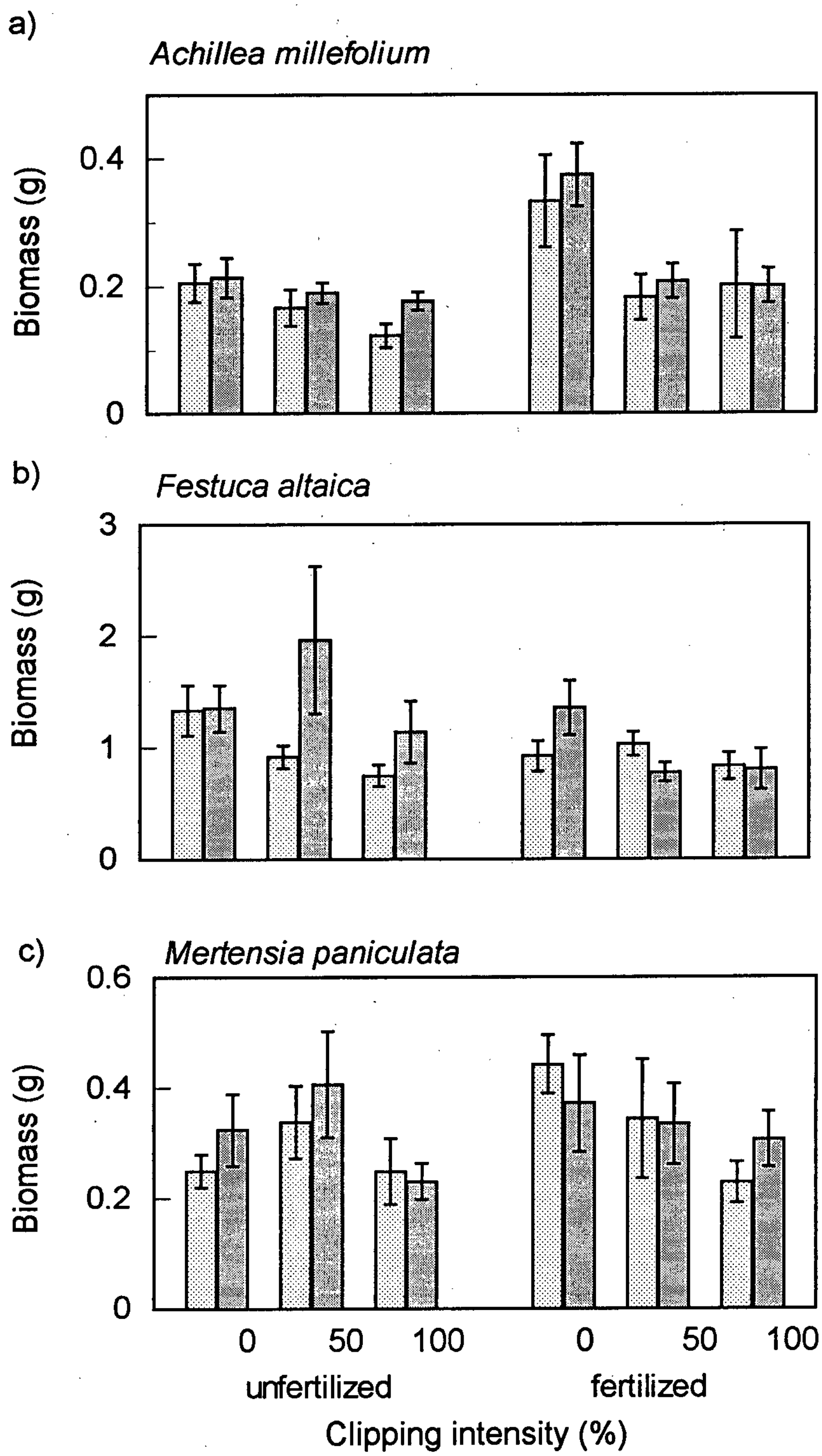


Figure 27. Mean (+/- 1 SE) below-ground biomass per plant, of long-term fertilized (▩) and unfertilized (□) plants, 75 days after transplanting, for three species at three intensities of clipping (0%, 50% and 100% leaf loss) and two levels of short-term fertilization.

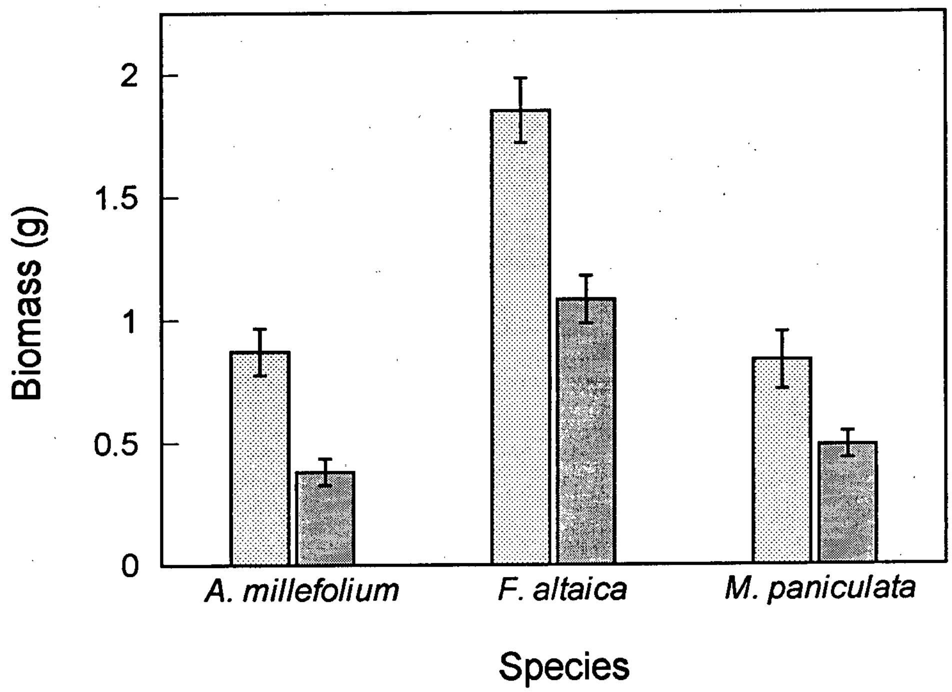


Figure 28. Mean (+/- 1 SE) total biomass per plant, of 100%-clipped (▩) and unclipped (▨) plants of *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*, 75 days after transplanting.

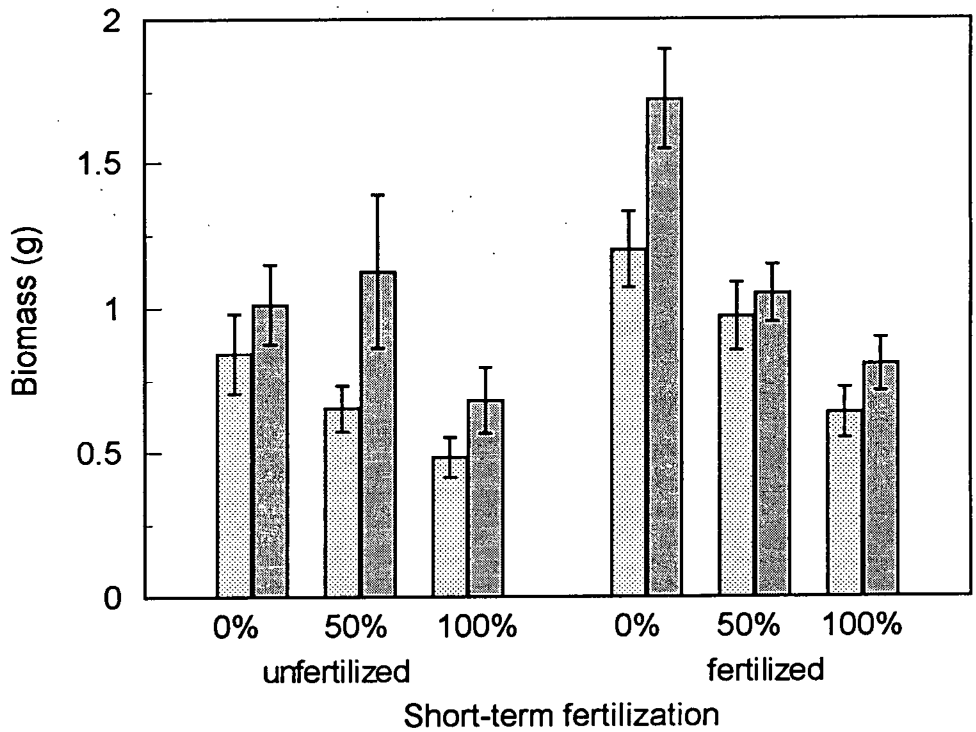


Figure 29. Mean (+/- 1 SE) total biomass per plant, of long-term fertilized (▨) and unfertilized (□) plants of all species, 75 days after transplanting, for three intensities of clipping (0%, 50% and 100% leaf loss) and two levels of short-term fertilization.

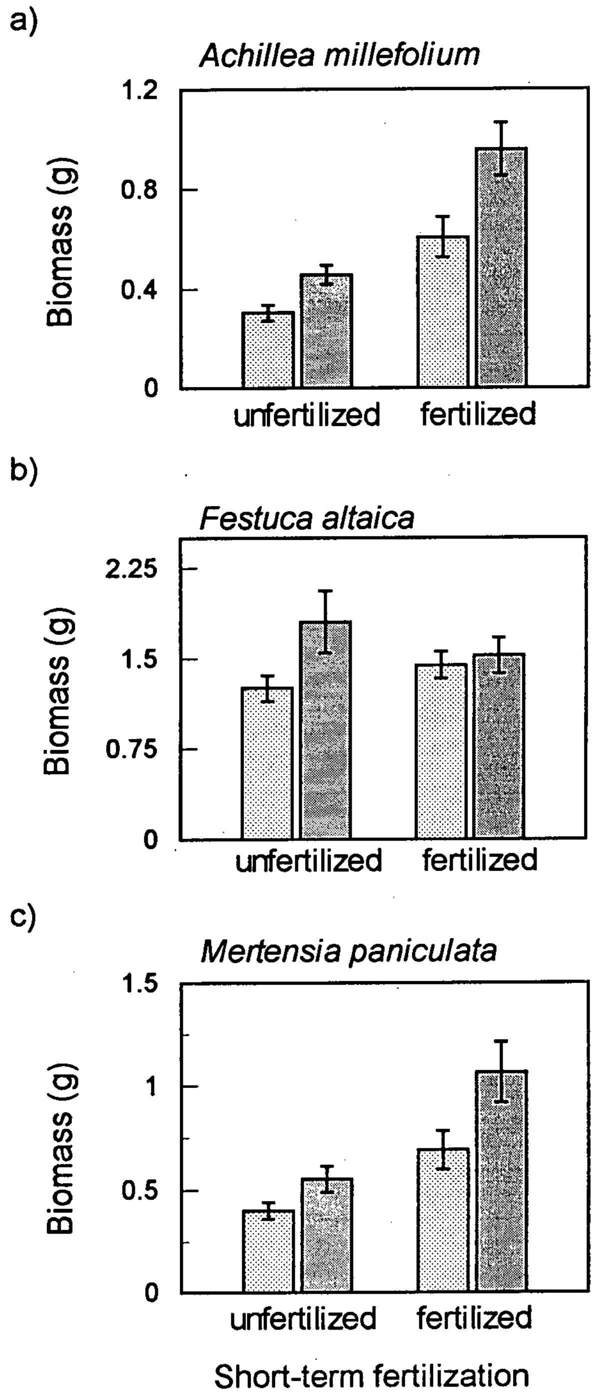


Figure 30. Mean (+/- 1 SE) total biomass per plant, of long-term fertilized (▩) and unfertilized (□) plants, 75 days after transplanting, at two levels of short-term fertilization.

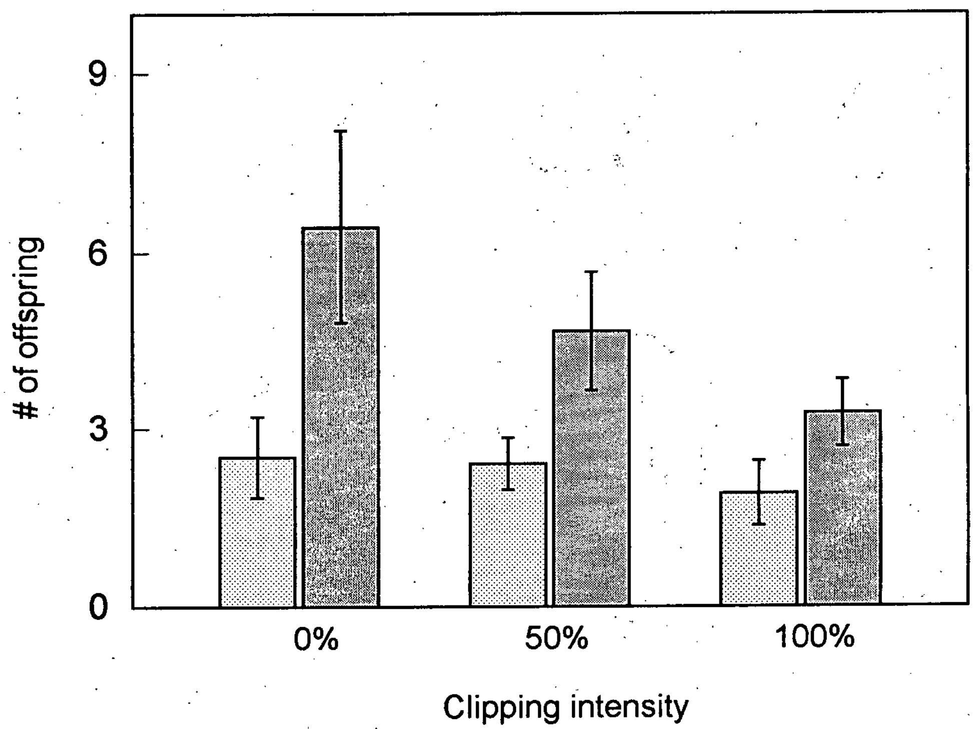


Figure 31. Mean (+/- 1 SE) number of vegetative offspring per plant, of short-term fertilized (▩) and unfertilized (▨) plants of all species, at three intensities of clipping (0%, 50% and 100% leaf loss).

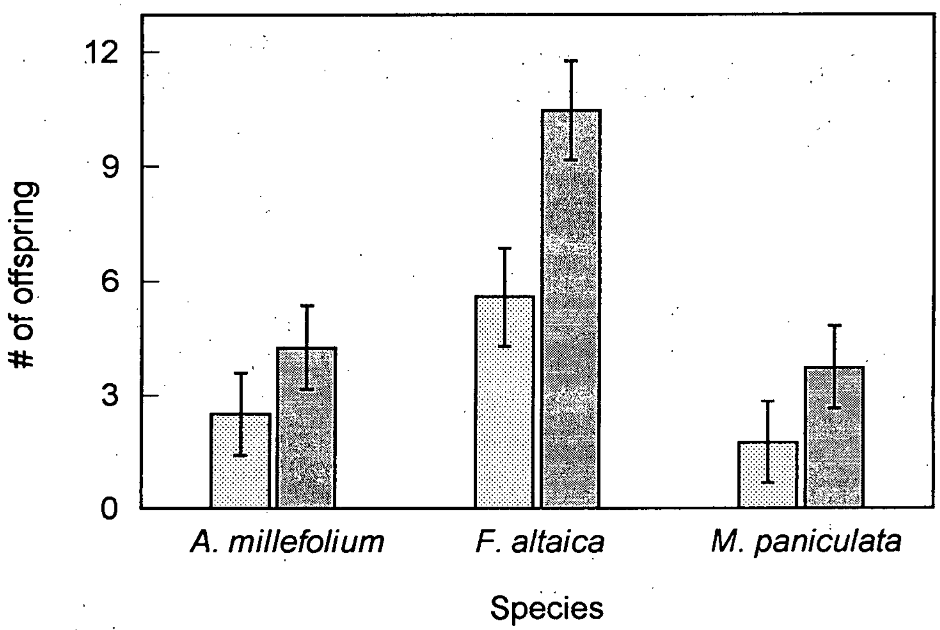


Figure 32. Mean (+/- 1 SE) number of vegetative offspring per plant, of short-term fertilized ( ) and unfertilized ( ) plants of *Achillea millefolium*, *Festuca altaica* and *Mertensia paniculata*.

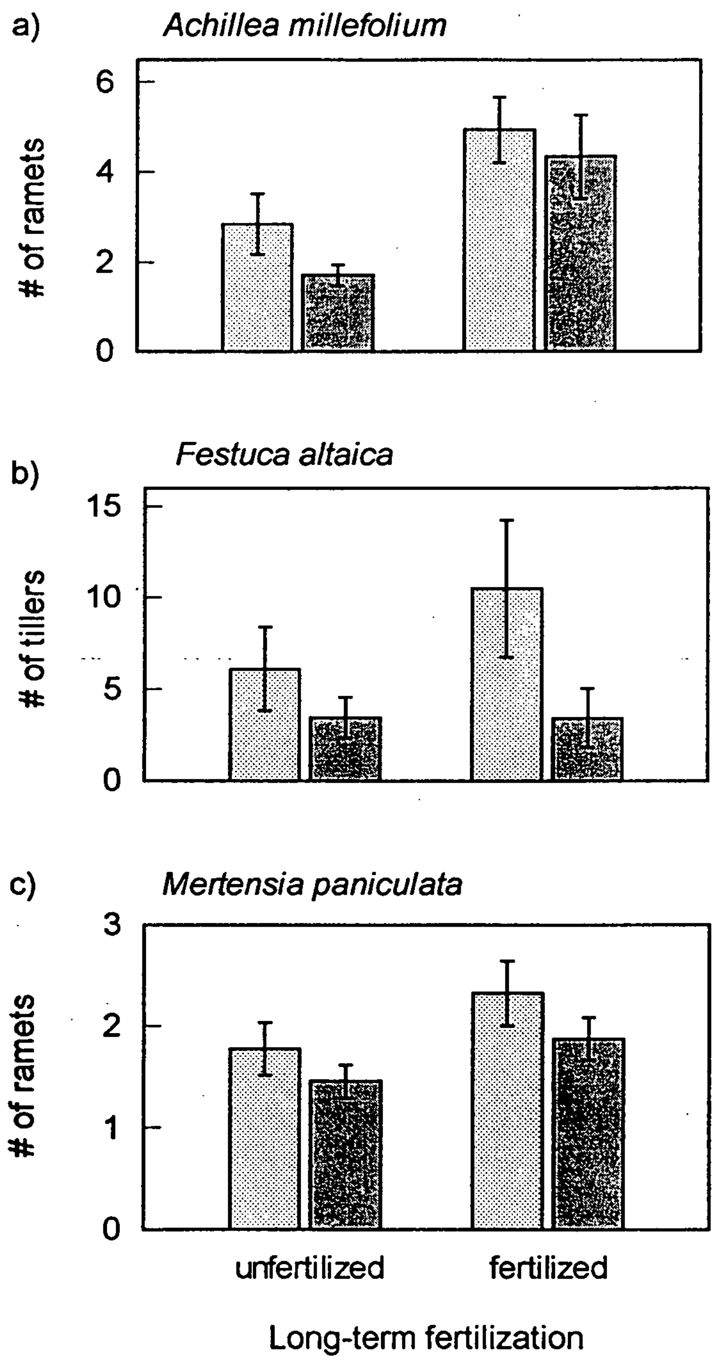


Figure 33. Mean number of vegetative offspring per plant, of 100%-clipped (▩) and unclipped (□) plants of all species, at two levels of long-term fertilization.

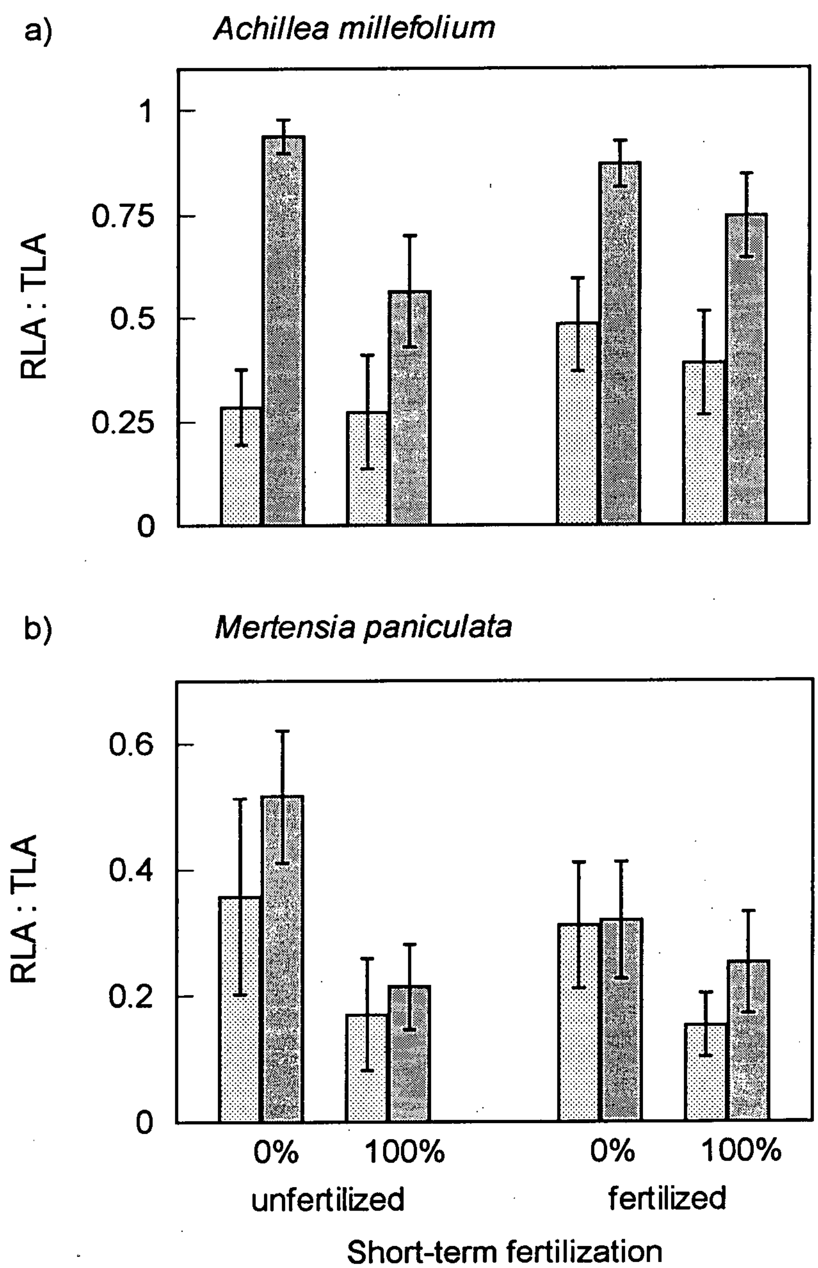


Figure 34. Mean (+/- 1 SE) ratio of ramet leaf area (RLA) : total plant leaf area (TLA), per plant, for long-term fertilized (▩) and unfertilized (▨) plants of two species, at two intensities of clipping (0% and 100% leaf loss), and two levels of short-term fertilization.

Appendix 1a. A key to the orthogonal contrast statements used for relative growth rate (RGR). Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP). Statements apply to all variables. Where applicable, FS can be replaced by FL in the statements. This appendix does not include all possible contrast statements, only those pertinent to the present study.

Contrast statement	Question
C	
0% vs 50%	Is there a difference in RGR between plants with 0% leaf loss compared to plants with 50 % leaf loss?
S	
FA vs (AM & MP)	Is there a difference in RGR between *F. altaica* and the two dicot species combined?
S	
AM vs MP	Is there a difference in RGR between *A. millefolium* and *M. paniculata*?
C x FS	
(0% vs 50%) x FS	Is the effect of 50% leaf loss on RGR, dependent on short-term fertilization?
C x S	
(0% vs 100%) x (AM vs FA)	Is the effect of 100% leaf loss on RGR, different for *A. millefolium* and *F. altaica* ?
FS x S	
(AM vs MP) x FS	Is the difference in RGR between *A. millefolium* and *M. paniculata*, dependent on short-term fertilization?
C x FS x FL	
(0% vs 100%) x FS x FL	Is the effect of 100% leaf loss on RGR, different for short-term fertilized and unfertilized plants, and is this difference dependent on long-term fertilization?
C x FS x S	
(0% vs 100%) x FL x (AM vs FA)	Is the effect of 100% leaf loss on RGR, different for *A. millefolium* and *F. altaica,* and is this difference dependent on short-term fertilization?
FS x FL x S	
FS x FL x (AM vs MP)	Is the difference in RGR between *A. millefolium* and *M. paniculata* different for short-term fertilized and short-term unfertilized plants, and is this difference dependent on long-term fertilization?

Contrast statement	Question
C x FS x FL x S (0% vs 100%) x FS x FL x (AM vs MP)	Is the effect of 100% leaf loss on RGR, different for short-term fertilized and unfertilized plants and is this difference dependent on long-term fertilization in the same manner for *A. millefolium* compared to *M. paniculata*?

Appendix 1b. Summary of ANOVA contrasts for the relative growth rate of leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	0.02849	20.66	**0.0001**
50% vs 100%	1	1.5642	1403.76	**0.0001**
S				
(FA vs AM & MP)	1	0.52360	379.74	**0.0001**
(AM vs MP)	1	1.34593	974.44	**0.0001**
C x FS				
(0% vs 50%) x FS	1			
(0% vs 100%) x FS	1	0.01133	8.22	**0.0044**
C x FL				
(0% vs 50%) x FL	1	0.00371	2.69	0.1020
(0% vs 100%) x FL	1	0.00536	3.89	**0.0495**
C x S				
(0% vs 100%) x (AM vs FA)	1	0.01413	10.25	**0.0015**
(0% vs 100%) x (AM vs MP)	1	1.72148	1248.5	**0.0001**
(0% vs 100%) x (FA vs MP)	1	1.29803	941.4	**0.0001**
FS x S				
(FA vs AM & MP) x FS	1	0.00659	4.78	**0.0294**
(AM vs MP) x FS	1	0.01379	10.0	**0.0017**
FL x S				
(FA vs AM & MP) x FL	1	0.00289	2.1	0.1486
(AM vs MP) x FL	1	0.00545	3.95	**0.0476**
C x FS x FL				
(0% vs 50%) x FS x FL	1	0.00005	0.03	0.854
(0% vs 100%) x FS x FL	1	0.00005	0.04	0.8515
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	0.00005	0.04	0.8478
(0% vs 100%) x FS x (AM vs MP)	1	0.01155	8.37	**0.0041**
(0% vs 100%) x FS x (FA vs MP)	1	0.00918	6.66	**0.0103**
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	0.01168	8.48	**0.0038**
(0% vs 100%) x FL x (AM vs MP)	1	0.00552	4.0	**0.0463**
(0% vs 100%) x FL x (FA vs MP)	1	0.00111	0.81	0.3702
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.00304	2.21	0.1382
FS x FL x (AM vs MP)	1	0.01193	8.65	**0.0035**

Note: For bold-typed values, $P < 0.05$.

Appendix 2. Summary of ANOVA contrasts for proportional final leaf area of clipped plants relative to controls. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
S				
(FA vs AM & MP)	1	0.00722	0.46	0.5006
(AM vs MP)	1	0.00916	0.58	0.4478
C x S				
C x (FA vs AM & MP)	1	0.00444	0.28	0.5969
C x (AM vs MP)	1	0.02271	1.43	0.2327
FS x S				
(FA vs AM & MP) x FS	1	0.02986	1.88	0.1714
(AM vs MP) x FS	1	0.02068	1.31	0.2547
FL x S				
(FA vs AM & MP) x FL	1	0.00399	0.25	0.6162
(AM vs MP) x FL	1	0.00332	0.21	0.6478
C x FS x S				
C x FS x (FA vs AM & MP)	1	0.00913	0.58	0.4488
C x FS x (AM vs MP)	1	0.03831	2.42	0.1216
C x FL x S				
C x FL x (FA vs AM & MP)	1	0.07494	4.73	**0.0309**
C x FL x (AM vs MP)	1	0.04933	3.11	0.0792
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.00215	0.14	0.7129
FS x FL x (AM vs MP)	1	0.00271	0.17	0.6794

Note: For bold-typed values, $P < 0.05$.

Appendix 3. Summary of ANOVA contrasts for proportional above-ground biomass of clipped plants relative to controls. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
S				
(FA vs AM & MP)	1	0.06157	0.31	0.5769
(AM vs MP)	1	1.14274	5.79	**0.0170**
C x S				
C x (FA vs AM & MP)	1	0.30414	1.54	0.2157
C x (AM vs MP)	1	0.10145	0.51	0.4740
FS x S				
(FA vs AM & MP) x FS	1	2.44767	12.4	**0.0005**
(AM vs MP) x FS	1	0.24121	1.22	0.2700
FL x S				
(FA vs AM & MP) x FL	1	0.000233	0.001	0.9726
(AM vs MP) x FL	1	0.099799	0.51	0.4777
C x FS x S				
C x FS x (FA vs AM & MP)	1	1.00186	5.08	**0.0253**
C x FS x (AM vs MP)	1	0.37287	1.89	0.1706
C x FL x S				
C x FL x (FA vs AM & MP)	1	0.24021	1.22	0.2710
C x FL x (AM vs MP)	1	0.04125	0.21	0.6479
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.12087	0.61	0.4346
FS x FL x (AM vs MP)	1	0.09894	0.50	0.4796

Note: For bold-typed values, $P < 0.05$.

Appendix 4. Summary of ANOVA contrasts for proportional below-ground biomass of clipped plants relative to controls. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
S				
(FA vs AM & MP)	1	0.02012	1.31	0.2542
(AM vs MP)	1	0.01865	1.21	0.2722
C x S				
C x (FA vs AM & MP)	1	0.15073	0.98	0.3234
C x (AM vs MP)	1	0.00608	0.40	0.5303
FS x S				
(FA vs AM & MP) x FS	1	0.10018	6.55	**0.0112**
(AM vs MP) x FS	1	0.05023	3.26	0.0722
FL x S				
(FA vs AM & MP) x FL	1	0.01413	0.92	0.3390
(AM vs MP) x FL	1	0.00386	0.25	0.6172
C x FS x S				
C x FS x (FA vs AM & MP)	1	0.01578	1.03	0.3123
C x FS x (AM vs MP)	1	0.02171	1.41	0.2363
C x FL x S				
C x FL x (FA vs AM & MP)	1	0.00040	0.03	0.8723
C x FL x (AM vs MP)	1	0.00235	0.15	0.6965
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.04181	2.72	0.1008
FS x FL x (AM vs MP)	1	0.03934	2.56	0.1113

Note: For bold-typed values, $P < 0.05$.

Appendix 5. Summary of ANOVA contrasts for proportional total biomass of clipped plants relative to controls. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
S				
(FA vs AM & MP)	1	0.00895	0.75	0.3890
(AM vs MP)	1	0.02580	2.15	0.1442
C x S				
C x (FA vs AM & MP)	1	0.01607	1.34	0.2487
C x (AM vs MP)	1	0.00006	0.01	0.9431
FS x S				
(FA vs AM & MP) x FS	1	0.08605	7.17	**0.0080**
(AM vs MP) x FS	1	0.02004	1.67	0.1978
FL x S				
(FA vs AM & MP) x FL	1	0.00239	0.20	0.6562
(AM vs MP) x FL	1	0.00479	0.40	0.5282
C x FS x S				
C x FS x (FA vs AM & MP)	1	0.00239	1.99	0.1597
C x FS x (AM vs MP)	1	0.00893	0.74	0.3893
C x FL x S				
C x FL x (FA vs AM & MP)	1	0.00013	0.01	0.9160
C x FL x (AM vs MP)	1	0.00171	0.14	0.7063
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.00706	0.59	0.4440
FS x FL x (AM vs MP)	1	0.01511	1.26	0.2632

Note: For bold-typed values, $P < 0.05$.

Appendix 6. Summary of ANOVA contrasts for the ratio of above-ground biomass per plant to total biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	259.48	4.03	**0.0454**
50% vs 100%	1	1914.51	29.76	**0.0001**
S				
(FA vs AM & MP)	1	17494.47	271.95	**0.0001**
(AM vs MP)	1	2573.65	40.01	**0.0001**
C x FS				
(0% vs 50%) x FS	1	171.59	2.67	0.1033
(0% vs 100%) x FS	1	5.99	0.09	0.7604
C x FL				
(0% vs 50%) x FL	1	6.54	0.10	0.75
(0% vs 100%) x FL	1	23.02	0.36	0.5501
C x S				
(0% vs 100%) x (AM vs FA)	1	53.60	0.83	0.3620
(0% vs 100%) x (AM vs MP)	1	38.22	0.59	0.4413
(0% vs 100%) x (FA vs MP)	1	175.75	2.73	0.0992
FS x S				
(FA vs AM & MP) x FS	1	47.18	0.73	0.3923
(AM vs MP) x FS	1	45.39	0.71	0.4015
FL x S				
(FA vs AM & MP) x FL	1	1148.04	17.85	**0.0001**
(AM vs MP) x FL	1	112.53	1.75	0.1868
C x FS x FL				
(0% vs 50%) x FS x FL	1	29.35	0.46	0.4998
(0% vs 100%) x FS x FL	1	18.43	0.29	0.5928
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	1.89	0.03	0.8641
(0% vs 100%) x FS x (AM vs MP)	1	5.32	0.08	0.7738
(0% vs 100%) x FS x (FA vs MP)	1	13.18	0.20	0.6511
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	3.12	0.05	0.8258
(0% vs 100%) x FL x (AM vs MP)	1	120.93	1.88	0.1712
(0% vs 100%) x FL x (FA vs MP)	1	160.73	2.5	0.1148
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	13.38	0.21	0.6486
FS x FL x (AM vs MP)	1	31.21	0.49	0.4865

Note: For bold-typed values, $P < 0.05$.

Appendix 7. Summary of ANOVA contrasts for the absolutepost-clipping growth of leaf area. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
F. altaica **C**				
0% vs 50%	1	13007.38	2.2	0.1388
50% vs 100%	1	11275.27	1.91	0.168
S				
(FA vs AM & MP)	1	535.43	0.09	0.7636
(AM vs MP)	1	754704.9	127.75	**0.0001**
C x FS				
(0% vs 50%) x FS	1	24280.86	4.11	**0.0434**
(0% vs 100%) x FS	1	117668.4	19.92	**0.0001**
C x FL				
(0% vs 50%) x FL	1	2017.6	0.34	0.5594
(0% vs 100%) x FL	1	1187.7	0.2	0.6542
C x S				
(0% vs 100%) x (AM vs FA)	1	3173.1	0.54	0.4642
(0% vs 100%) x (AM vs MP)	1	514.9	0.09	0.768
(0% vs 100%) x (FA vs MP)	1	1076.0	0.18	0.6698
FS x S				
(FA vs AM & MP) x FS	1	9718.36	1.65	0.2005
(AM vs MP) x FS	1	249328.4	42.2	**0.0001**
FL x S				
(FA vs AM & MP) x FL	1	59588.0	10.09	**0.0016**
(AM vs MP) x FL	1	71630.9	12.12	**0.0006**
C x FS x FL				
(0% vs 50%) x FS x FL	1	3504.2	0.59	0.4417
(0% vs 100%) x FS x FL	1	2856.2	0.48	0.4873
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	6078.4	1.03	0.3112
(0% vs 100%) x FS x (AM vs MP)	1	25505.7	4.32	**0.0385**
(0% vs 100%) x FS x (FA vs MP)	1	6229.9	1.05	0.3052
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	1129.6	0.19	0.6622
(0% vs 100%) x FL x (AM vs MP)	1	58.4	0.01	0.9208
(0% vs 100%) x FL x (FA vs MP)	1	1608.5	0.27	0.6022
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	11220.5	1.9	0.1691
FS x FL x (AM vs MP)	1	6134.9	1.04	0.3089

Note: For bold-typed values, $P < 0.05$.

Appendix 8 . Summary of ANOVA contrasts for absolute final leaf area per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	86238.5	11.56	**0.0008**
50% vs 100%	1	78112.3	10.22	**0.0015**
S				
(FA vs AM & MP)	1	50528.7	6.77	**0.0097**
(AM vs MP)	1	1120692.7	150.18	**0.0001**
C x FS				
(0% vs 50%) x FS	1	65507.1	9.35	**0.0024**
(0% vs 100%) x FS	1	121504.1	16.28	**0.0001**
C x FL				
(0% vs 50%) x FL	1	2357.8	0.32	0.5744
(0% vs 100%) x FL	1	5033.6	0.67	0.4121
C x S				
(0% vs 100%) x (AM vs FA)	1	85544.1	11.46	**0.0008**
(0% vs 100%) x (AM vs MP)	1	31161.3	4.18	**0.0418**
(0% vs 100%) x (FA vs MP)	1	12867.9	1.72	0.19
FS x S				
(FA vs AM & MP) x FS	1	13551.4	1.82	0.1787
(AM vs MP) x FS	1	260436.7	34.9	**0.0001**
FL x S				
(FA vs AM & MP) x FL	1	54396.42	7.29	**0.0073**
(AM vs MP) x FL	1	84393.8	11.31	**0.0009**
C x FS x FL				
(0% vs 50%) x FS x FL	1	6065.4	0.81	0.3679
(0% vs 100%) x FS x FL	1	5464.22	0.73	0.3928
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	4314.5	0.58	0.4476
(0% vs 100%) x FS x (AM vs MP)	1	33649.4	4.51	**0.0344**
(0% vs 100%) x FS x (FA vs MP)	1	12967.2	1.74	0.1883
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	1566.9	0.21	0.6471
(0% vs 100%) x FL x (AM vs MP)	1	69.52	0.01	0.9232
(0% vs 100%) x FL x (FA vs MP)	1	926.31	0.12	0.7248
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	6427.0	0.86	0.3541
FS x FL x (AM vs MP)	1	6427.0	0.86	0.3541

Note: For bold-typed values, $P < 0.05$.

Appendix 9. Summary of ANOVA contrasts for absolute above-ground biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	2.95206	34.13	**0.0001**
50% vs 100%	1	1.52111	22.19	**0.0001**
S				
(FA vs AM & MP)	1	0.21172	2.79	0.0957
(AM vs MP)	1	0.0003	0.00	0.9493
C x FS				
(0% vs 50%) x FS	1	0.76525	9.35	**0.0024**
(0% vs 100%) x FS	1	2.02602	26.7	**0.0001**
C x FL				
(0% vs 50%) x FL	1	0.24611	3.24	0.0726
(0% vs 100%) x FL	1	0.42083	5.54	**0.0191**
C x S				
(0% vs 100%) x (AM vs FA)	1	0.00753	0.10	0.7529
(0% vs 100%) x (AM vs MP)	1	0.19789	2.61	0.1072
(0% vs 100%) x (FA vs MP)	1	0.27954	3.68	0.0557
FS x S				
(FA vs AM & MP) x FS	1	0.31584	4.16	**0.0421**
(AM vs MP) x FS	1	0.04242	0.56	0.4552
FL x S				
(FA vs AM & MP) x FL	1	0.86731	11.43	**0.0008**
(AM vs MP) x FL	1	0.00334	0.04	0.8339
C x FS x FL				
(0% vs 50%) x FS x FL	1	0.12703	1.67	0.1966
(0% vs 100%) x FS x FL	1	0.12151	1.6	0.2066
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	0.22471	2.96	0.0862
(0% vs 100%) x FS x (AM vs MP)	1	0.02349	0.31	0.5783
(0% vs 100%) x FS x (FA vs MP)	1	0.09757	1.29	0.2576
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	0.05978	0.79	0.3754
(0% vs 100%) x FL x (AM vs MP)	1	0.07686	1.01	0.3149
(0% vs 100%) x FL x (FA vs MP)	1	0.00133	0.02	0.8946
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.36975	4.87	**0.0279**
FS x FL x (AM vs MP)	1	0.01155	0.15	0.6967

Note: For bold-typed values, $P < 0.05$.

Appendix 10. Summary of ANOVA contrasts for absolute below-ground biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	0.12281	0.53	0.4654
50% vs 100%	1	1.32481	4.57	**0.0332**
S				
(FA vs AM & MP)	1	64.2931	226.32	**0.0001**
(AM vs MP)	1	0.76477	2.69	0.1017
C x FS				
(0% vs 50%) x FS	1	0.73223	2.63	0.1058
(0% vs 100%) x FS	1	0.02891	0.1	0.7499
C x FL				
(0% vs 50%) x FL	1	0.06146	0.22	0.6421
(0% vs 100%) x FL	1	0.00185	0.01	0.9357
C x S				
(0% vs 100%) x (AM vs FA)	1	0.74047	2.61	0.1073
(0% vs 100%) x (AM vs MP)	1	0.00331	0.01	0.9141
(0% vs 100%) x (FA vs MP)	1	0.81323	2.86	0.0915
FS x S				
(FA vs AM & MP) x FS	1	2.71123	9.54	**0.0022**
(AM vs MP) x FS	1	0.01949	0.07	0.7935
FL x S				
(FA vs AM & MP) x FL	1	1.48664	5.23	**0.0227**
(AM vs MP) x FL	1	0.002	0.01	0.9332
C x FS x FL				
(0% vs 50%) x FS x FL	1	1.26184	4.44	**0.0358**
(0% vs 100%) x FS x FL	1	0.18739	0.66	0.4172
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	0.07961	0.28	0.5969
(0% vs 100%) x FS x (AM vs MP)	1	0.00027	0.00	0.9752
(0% vs 100%) x FS x (FA vs MP)	1	0.08609	0.3	0.5823
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	0.01010	0.04	0.8506
(0% vs 100%) x FL x (AM vs MP)	1	0.00155	0.01	0.9411
(0% vs 100%) x FL x (FA vs MP)	1	0.01902	0.07	0.7960
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	1.03611	3.65	0.0570
FS x FL x (AM vs MP)	1	0.00548	0.02	0.8896

C x FS x FL x S				
(0% vs 50%) x FS x FL x (FA vs AM & MP)	1	2.85251	10.04	**0.0017**
(0% vs 50%) x FS x FL x (AM vs MP)	1	0.01097	0.04	0.8498
(0% vs 100%) x FS x FL x (FA vs AM & MP)	1	0.78787	2.77	0.0967
(0% vs 100%) x FS x FL x (AM vs MP)	1	0.09163	0.32	0.5704

Note: For bold-typed values, $P < 0.05$.

Appendix 11. Summary of ANOVA contrasts for absolute total biomass per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	3.99461	9.19	**0.0026**
50% vs 100%	1	5.19867	13.68	**0.0003**
S				
(FA vs AM & MP)	1	71.88133	165.45	**0.0001**
(AM vs MP)	1	0.73382	1.69	0.1946
C x FS				
(0% vs 50%) x FS	1	2.75664	6.7	**0.01**
(0% vs 100%) x FS	1	2.53891	5.84	**0.0161**
C x FL				
(0% vs 50%) x FL	1	0.06143	0.14	0.7071
(0% vs 100%) x FL	1	0.47850	1.1	0.2947
C x S				
(0% vs 100%) x (AM vs FA)	1	0.89736	2.07	0.1515
(0% vs 100%) x (AM vs MP)	1	0.25238	0.58	0.4465
(0% vs 100%) x (FA vs MP)	1	2.04636	4.71	**0.0306**
FS x S				
(FA vs AM & MP) x FS	1	4.87874	11.23	**0.0009**
(AM vs MP) x FS	1	0.00438	0.01	0.9201
FL x S				
(FA vs AM & MP) x FL	1	0.08282	0.19	0.6627
(AM vs MP) x FL	1	0.00017	0.00	0.9844
C x FS x FL				
(0% vs 50%) x FS x FL	1	2.18898	5.04	**0.0254**
(0% vs 100%) x FS x FL	1	0.61069	1.41	0.2366
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	0.57182	1.32	0.2520
(0% vs 100%) x FS x (AM vs MP)	1	0.01869	0.04	0.8358
(0% vs 100%) x FS x (FA vs MP)	1	0.36695	0.84	0.3587
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	0.02074	0.05	0.8272
(0% vs 100%) x FL x (AM vs MP)	1	0.10028	0.23	0.6312
(0% vs 100%) x FL x (FA vs MP)	1	0.03043	0.07	0.7914
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	2.64412	6.09	**0.0141**
FS x FL x (AM vs MP)	1	0.00109	0.00	0.9600

Note: For bold-typed values, $P < 0.05$.

Appendix 12. Summary of ANOVA contrasts for vegetative reproduction per plant. Species (S), long-term fertilization (FL), short-term fertilization (FS) and clipping effect (C). *Achillea millefolium* (AM), *Festuca altaica* (FA) and *Mertensia paniculata* (MP).

Contrast	df	Contrast SS	F value	Pr > F
C				
0% vs 50%	1	0.35442	3.43	0.0648
50% vs 100%	1	1.03149	9.99	**0.0017**
S				
(FA vs AM & MP)	1	11.24031	108.82	**0.0001**
(AM vs MP)	1	3.06874	29.71	**0.0001**
C x FS				
(0% vs 50%) x FS	1	0.22723	2.2	**0.0438**
(0% vs 100%) x FS	1	0.44751	4.31	**0.0387**
C x FL				
(0% vs 50%) x FL	1	0.48023	4.65	**0.0317**
(0% vs 100%) x FL	1	0.01762	0.17	0.6798
C x S				
(0% vs 100%) x (AM vs FA)	1	0.57795	5.6	**0.0185**
(0% vs 100%) x (AM vs MP)	1	0.03520	0.34	0.5597
(0% vs 100%) x (FA vs MP)	1	0.87070	8.43	**0.0039**
FS x S				
(FA vs AM & MP) x FS	1	3.97226	38.46	**0.0001**
(AM vs MP) x FS	1	0.43062	4.17	**0.0419**
FL x S				
(FA vs AM & MP) x FL	1	0.23382	2.26	0.1333
(AM vs MP) x FL	1	0.81351	7.88	**0.0053**
C x FS x FL				
(0% vs 50%) x FS x FL	1	0.00277	0.03	0.8699
(0% vs 100%) x FS x FL	1	0.00210	0.02	0.8868
C x FS x S				
(0% vs 100%) x FS x (AM vs FA)	1	0.03227	0.31	0.5765
(0% vs 100%) x FS x (AM vs MP)	1	0.05276	0.51	0.4752
(0% vs 100%) x FS x (FA vs MP)	1	0.16429	1.59	0.2081
C x FL x S				
(0% vs 100%) x FL x (AM vs FA)	1	0.51856	5.02	**0.0257**
(0% vs 100%) x FL x (AM vs MP)	1	0.08735	0.85	0.3584
(0% vs 100%) x FL x (FA vs MP)	1	0.16965	1.64	0.2008
FS x FL x S				
FS x FL x (FA vs AM & MP)	1	0.00998	0.10	0.7561
FS x FL x (AM vs MP)	1	0.04793	0.46	0.4962

Note: For bold-typed values, $P < 0.05$.