FACTORS RESTRICTING PLANT GROWTH
IN A BOREAL FOREST UNDERSTORY:
A FIELD TEST OF THE RELATIVE IMPORTANCE OF
ABIOTIC AND BIOTIC FACTORS

by

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Abstract

This study tests some of the conflicting predictions made by Grime (1977, 1979) and Tilman (1982, 1988) on how competition intensity changes along a gradient of nutrient availability. This was tested by applying three levels of nutrients (fertilizer treatments) and by varying the amount of neighbors present (competition treatments) in a factorial design using five common herbaceous species found in the boreal forest understory (*Achillea millefolium, Anemone parviflora, Festuca altaica, Lupinus arcticus, Mertensia paniculata*). Competition intensity indices (CI) were calculated from the final biomass and leaf number for each species at all fertility levels.

Addition of fertilizer significantly increased biomass and leaf number of *A. millefolium* and *F. altaica*. *Anemone parviflora* had high mortality in fertilized plots, while *L. arcticus* and *M. paniculata* did not respond to fertilizer treatments. None of the species responded significantly to the varying amounts of neighbors present in the natural habitat. Competition intensity (CI) values were not significantly different from zero at any of the fertility levels for three out of the four species used to calculate CI. The results support neither of the original predictions made by Grime nor Tilman. However, the lack of response by these species is consistent with another of Grime's predictions based on his arguments about the evolution of stress-tolerance: i.e. his so-called 'stress-tolerant' species adapted to live in habitats of extremely low resource availability.

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Chapter 1. Introduction

Individuals or species living in nature are exposed to numerous factors which affect their growth. A major challenge for ecologists is to measure the relative strength of these factors, disentangle interactions among them, and use these to account for the distribution and abundance of species that we see in nature (Hunter and Price 1992). In community ecology, one of the central questions is to determine the relative importance of competition, predation, and the abiotic environment in structuring a community (Connell 1975; Keddy 1989).

One of these factors, competition, occurs when two or more individuals utilize the same limited resource. Since most higher plants require identical resources (light, mineral nutrients, and water) for their survival, it is very likely that competition plays a major role in structuring plant communities.

A central question in plant ecology has been how the intensity of competition (Weldon and Slauson 1986) is influenced by the availability of nutrients. Two conflicting predictions are prevalent in the literature. Grime (1973, 1977), Huston (1979), and Keddy (1989) argue that intensity of competition increases as nutrient level increases. In contrast, models proposed by Tilman (1982, 1988) predict that the intensity of competition remains constant along as nutrient levels change.

The main goal of this research was to conduct field tests of some of the conflicting predictions of these two models in the boreal forest understory. Conducting the experiment in the boreal forest understory was beneficial since most of the recent field tests in an

attempt to clarify the controversy have been mainly done in temperate grasslands and pastures. The experiment was done by applying different amounts of fertilizer to the herbaceous understory species of the boreal forest and measuring the intensity of competition on selected species at each nutrient level.

A. Models of Grime and Tilman

Today, the importance of competition in structuring plant communities is well accepted by a majority of ecologists (see reviews by Connell 1983; Schoener 1983; Golberg and Barton 1992; Gurevitch 1992). However, our ability to predict the outcome of competition and to identify the relative importance of competition in structuring plant communities is still limited (Grime 1977, 1987; Tilman 1982, 1987a, 1988; Wilson and Keddy 1986a; Thompson and Grime 1988; Goldberg 1990; Grace 1990). A variety of approaches have been used to predict the competitive outcome (Grace 1990). Among them, the two most widely discussed in plant ecology are the models proposed by Grime (1977, 1979) and Tilman (1982, 1988), which sometimes make conflicting predictions.

One of the debated issues is whether the intensity of competition varies along a gradient of nutrient availability. Grime (1977, 1979) argues that competition intensity increases along such a gradient, while Tilman (1982, 1988) predicts that competition intensity should be equally intense along a nutrient availability gradient. In the following sections, the basis of the two conflicting predictions are briefly reviewed.

1. Grime's model

Grime (1977, 1979) refined the theory of r- and K-selection (MacArthur and Wilson 1967) and proposed a life history strategy developed only for plants (Grace 1990). According to his model, the degree of "stress[1]" and "disturbance[2]" to which the plants are adapted determines their life history characteristics. Although disturbance is a major component of Grime's model, it will not be referred to here.

An important notion of Grime's model is the evolutionary tradeoff between the ability to exploit resources rapidly and the ability to tolerate high stress. Grime argues that this tradeoff in abilities causes physiological constraints on plants which prohibit them from having both extreme abilities (Grace 1990), although intermediate characteristics may exist. According to Grime's classification, species with a high ability to capture resources and with a high maximum relative growth rate (RGR_{max}) are referred to as "competitors". In contrast, species with tolerance to high stress and with a low RGR_{max} are referred to as "stress-tolerators". Therefore, habitats with low stress are likely to be dominated by competitors, habitats with high stress by stress-tolerators, and intermediate habitats by plants with intermediate characteristics (Chapin 1980).

Grime's definition of competitive ability correlates positively with the ability to capture resources, and negatively with the ability to tolerate high stress (Grace 1990). In other words, the competitive ability of "competitors" is high while it is low for "stress-tolerators". By definition, the competition intensity in a habitat increases as species with

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[1] Phenomena which restrict photosynthetic production (e.g. temperature, moisture).

[2] Any factor associated with partial or total reduction of plant biomass (e.g. herbivory, fire).

higher competitive ability occupy the site. Thus, competition intensity in a highly stressful habitat is low because it is dominated by poorly competitive "stress-tolerators". However, in a less stressful habitat competition intensity increases as "competitors" are the dominant occupants.

Grime's argument that competition intensity increases along a gradient of decreasing stress may also be applied even if it does not involve a change in species composition. When an individual is grown in a less stressful environment, it is likely to increase its biomass resulting in greater demand for resources and higher ability to capture resources due to its size. This is likely to cause higher competition intensity.

Both Grime and Tilman focus on the influence of nutrient availability on competition intensity. From these arguments, Grime's model predicts that competition intensity will be higher as nutrient availability increases.

2. Tilman's model

Tilman (1982, 1988) proposed a resource-based theory of competition. It is assumed that when resources are exploited by plants, the concentration is drawn down to a level R*, which is defined as the equilibrium resource concentration or the level below which the population is unable to maintain itself (Grace 1990). The species with lowest R* will competitively displace all other species at equilibrium.

Tilman considers evolutionary tradeoffs in terms of the relative ability of a species to compete for different ratios of resources (Grace 1990). Tradeoffs in biomass allocation to roots, stems, and leaves, for example, result in straightforward tradeoffs in individuals'

abilities to compete for different resources. Based on this argument, in habitats with very low nutrient availability, competition occurs primarily for soil resources as species allocate biomass to roots to exploit limited nutrients. However, in habitats where nutrients are more available, vegetation will form a dense canopy and light becomes the limiting factor for growth. In this situation, those species that are able to allocate biomass to shoots to intercept more light become favorable.

From these arguments, it is predicted that competition in nutrient-poor habitats is mainly belowground while in nutrient-rich habitats it is mainly aboveground. Due to this tradeoff between above- and below-ground competition along a gradient of increasing nutrient availability, Tilman predicts overall competition intensity to remain constant along the gradient.

3. The controversy

Different arguments as to the evolutionary tradeoff of plant traits which would be favorable in a certain habitat underlie the Grime vs. Tilman debate over the intensity of competition along a nutrient availability gradient. Grime and Campbell (1991) and Grime (1994) question the validity of Tilman's predictions by arguing that he underestimates the interdependence of above- and below-ground growth. However, evidence to support both evolutionary tradeoffs has been reported (Grime 1994; Mahmoud and Grime 1976; Tilman 1984, 1987b).

Recent attempts to clarify the conflicting predictions of Grime and Tilman have focused on semantic problems (Goldberg 1990; Grace 1990, 1991) and different measures of the intensity of competition (Grace 1993, 1995). However, intensity of competition along

a nutrient availability gradient still remains a controversial issue. Evidence to assess these two models is accumulating (DiTommaso and Aarssen 1991; Wilson and Tilman 1991,1993, 1995; Campbell and Grime 1992; Wedin and Tilman, 1993; Turkington et al., 1993; Belcher et al. 1995), but does not yet clarify the issue. Goldberg and Barton (1992) have reported that in studies using natural gradients, the intensity of competition seems to increase with higher nutrient availability which is consistent with Grime's predictions while in studies using experimental gradients (by applying fertilizer), Tilman's model seems to make more accurate predictions.

B. Objectives and predictions

In this section, four main objectives of this research and their predictions are discussed. This research was conducted in the boreal forest and five herbaceous species within the understory were selected (see Chapter 2) to test each of the following objectives.

a) Do natural nutrient levels limit plant growth, and if so, by how much?

Soils of the boreal forest have very low nutrient availability (Chapter 2). This may be an important direct factor in limiting plant growth.

Predictions

If the growth of boreal forest understory species were limited by nutrients, an increase in growth (i.e. biomass, leaf number) should be observed by application of fertilizer. This is predicted by both Grime and Tilman. However, Grime's model also predicts that if the species present in the understory are 'stress tolerators', applying fertilizer should have little or no immediate effect on the growth as they are well adapted to the low nutrient habitat and have very low RGR_{max}.

b) Does competition restrict plant growth in a natural habitat, and if so, by how much?

In this research, the effect of competition is determined by removing neighbors and measuring the increased growth of the remaining target individuals (Chapter 2).

Predictions

Both Grime and Tilman predict competition to be a factor in restricting plant growth in a natural habitat. The difference between the two predictions is what the plants compete for. Tilman predicts competition to be primarily for belowground resources in such a habitat, while Grime argues it would be competing for both above- and belowground resources. However, Grime also predicts that if the species in the understory are 'stress-tolerators', competition may not be a restricting factor since they have very low RGR_{max} and are not able to take advantage of the resources made available by removing neighbors.

c) Will the intensity of competition change along a nutrient availability gradient?

This is the main objective of my research and is an attempt to test some of Grime and Tilman's conflicting predictions. This research was designed to separate the relative effects of above- and belowground competition in restricting plant growth along a nutrient availability gradient (Chapter 2). Surprisingly, although the biomass allocation to roots and shoots has been at the center of Tilman's models and predictions, there have been relatively few studies that have attempted to separate the effects of above- and belowground competition.

Predictions

Grime predicts competition intensity, both above- and belowground, to increase along a gradient of increasing nutrient availability. However, if the understory species of the boreal forest are 'stress-tolerators', nutrient application would not increase the intensity of competition, provided there is no change in species composition. This is due to the fact that the 'stress-tolerators' are not efficient in taking advantage of the excess resources made available by adding fertilizer and by removing neighbors. Thus, competition intensity remains very low, and may not change along the gradient of nutrient application.

Tilman predicts total competition intensity to remain constant along the gradient of increasing nutrient availability. Grime's prediction based on the 'stress-tolerators' may also result in constant competition intensity, but Tilman predicts that competition is still a major factor and may be detected at any level of the gradient. Also, Tilman predicts a tradeoff between above- and belowground competition. Thus, aboveground (shoot) competition will

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be positively correlated, and belowground (root) competition will be negatively correlated with increasing nutrient availability.

d) Will the answers to the first two questions differ among various species within the community?

The limited empirical evidence available on Grime's and Tilman's predictions focus almost exclusively on the intensity of competition or response of individuals of one or a few species, not on the response of the entire community (reviewed in Goldberg and Barton 1992). In this study five species were selected to investigate whether they differed in their response to fertilizer addition and to the removal of their neighbors.

Predictions

Two kind of results may be predicted. First, species living in the same habitat might have converged to the same habitat conditions. Thus the result should be that all five species show the same response to fertilizing and neighbor removal treatments. In contrast, one could also argue that coexisting species should be 'different' in order to coexist in which case they should show different responses to the treatments. By observing the results of the first three questions, it is possible to determine if they differ in responses to the various treatments.

Chapter 2. Materials and methods

A. Study Site

1. The boreal forest

The boreal forest is one of the world's major vegetation regions, occupying 12×10^6 km^2 of the earth's surface (Leith 1975). It is a biome of variable latitudinal width and species composition, but similar overall character, that circles around the northern part of the world (Kimmins and Wein 1986, Fig. 1). To the south of the boreal forest lies the temperate forest, with a transitional zone of mixed species stands or a mosaic of temperate deciduous species (Apps et al. 1993). To the north lies subarctic woodlands which contains a mosaic of treeless patches and stunted forest stands (Apps et al. 1993).

1.1. Climatic characteristics

Although there is wide variability of climatic characteristics within the boreal forest, it is characterized by long cold winters, short warm summers, widely fluctuating day length, and low precipitation (Larsen 1980, Slaughter and Viereck 1986). Precipitation in Canadian boreal regions range between 25 and 36 cm annually which is only slightly above values typical of deserts (Kelsall et al. 1977). Mean annual minimum temperatures and maximum summer temperatures are quite uniform across the boreal region in North America, at approximately -45°C and 30°C, respectively (Kelsall et al. 1977). The growing
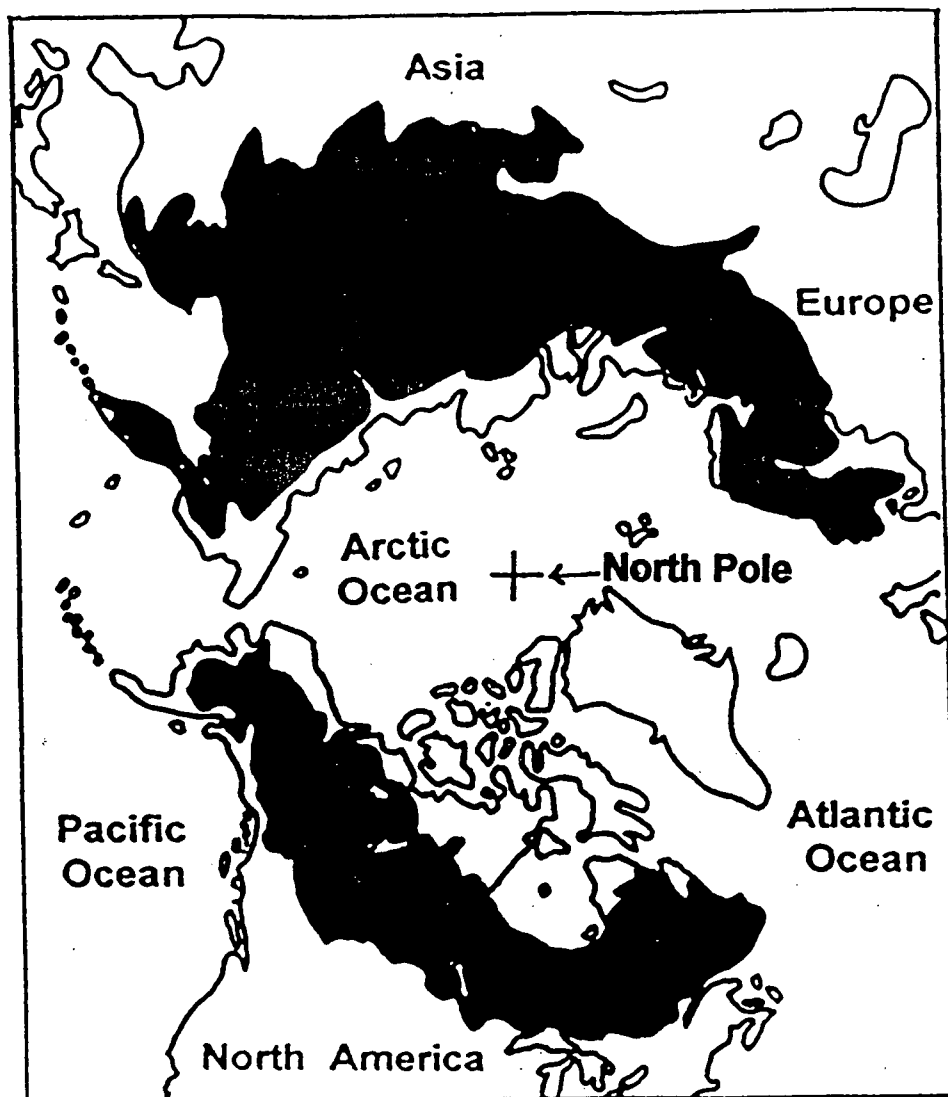
Fig. 1. Circumpolar distribution of the boreal forest.

season is generally short in the boreal region, becoming progressively shorter to the north (Van Cleve and Alexander 1981, Apps et al. 1993).

1.2 Soil characteristics

A major theme in this thesis concerns the relationship between competition and soil productivity. In the boreal forest understory, various factors have an influence on soil productivity. Here, some of these factors will be considered.

Soil temperature and moisture

Despite their variability, low soil temperature and high moisture content are two general characteristics of boreal forest soils. Soil temperatures are low, even during the summer, due to the small amount of solar radiation reaching the soil surface. High moisture is due to the fact that the combined amount of evaporation from the soil surface and the evapotranspiration from the plants are rarely in excess of precipitation (Larsen 1980). Low soil temperature and high moisture content together influence two of the major characteristics of boreal forest soils; podzolization and permafrost.

Podzolization

Podzolization is the movement of iron, aluminum, and organic materials, including organic chelating agents, from an upper A horizon to a lower B horizon, and the maintenance of these characteristic zones in a steady state equilibrium (Larsen 1980). The product of this

process is soil classified as podzol[3]. Although podzolization is not a exclusive process to the boreal region, it is observed throughout the boreal forest. The most intense podzolization occurs in the more northerly areas, as a consequence of lower soil and atmospheric temperatures, and higher moisture content (Larsen 1980).

Permafrost

Permanently frozen ground underlies a fifth of world's land surface and its presence impedes drainage and influences soils in a variety of ways (Larsen 1980). Between the perennially frozen underground material and the ground surface is an 'active layer' which freezes in winter and thaws in summer (Wahl et al. 1987) and the depth of the active layer becomes progressively shallower to the north in the boreal region. The depth of the active layer is crucial for plants as they require a certain soil volume for rooting and acquiring nutrients and water. In the boreal forest, compared to the tundra, the active layer in summer is sufficiently deep for trees such as *Picea mariana* Voss (black spruce) and *Picea glauca* (Moench) Voss (white spruce) which have shallow root systems (Larsen 1980).

Decomposition of organic material and nutrient availability

Another major characteristic of boreal forest soils is the amount of organic matter present overlying the mineral substrate (Larsen 1980). This is caused by the slow rate of decomposition which is mainly controlled by low soil temperature and quality of coniferous

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[3] A typical profile of this soil type is an infertile, light colored leached A layer, beneath a thick organic layer showing various stages of decomposition. Below the A layer, is the B layer with a dark appearance with accumulating oxides and clay (Larsen 1980).

tree needles (Larsen 1980). As a consequence, mineral nutrients are trapped in this thickened forest floor and become unavailable for plant use. Productivity of the boreal forest is known to be limited primarily by low soil fertility (Vitousek and Matson 1989)

The accumulated organic material also works as an insulator, which lowers the soil temperature even further. Thus, the active layer thins and the rate of decomposition decreases to an even lower level making the soil even less productive.

1.3 Fire

Fire results in drastic changes in ecosystem structure and function and is an integral feature of the boreal forest (Kelsall 1977). Particularly, fire has produced a mosaic of stand ages throughout the boreal region (Dyrness et al. 1986).

One of the consequence of fire is the release of nutrients trapped in the organic matter layer. All nutrients in the mineral soil increase in concentration after fire because of ash deposition. Dyrness and Norum (1983) reported that soil pH, amount of total phosphorus (P) and available P in the forest floor increased significantly after an experimental burn. Total nitrogen (N) increased significantly in the forest floor of moderately burned areas, but decreased in heavily burned areas probably due to volatilization. In general, the total amount of all nutrients available for recycling increases after a fire (Kelsall 1977).

Fire removes the accumulated organic layer and, by burning vegetation, it removes shade from canopies. It also blackens the soil surface (Dyrness et al. 1986) which improves

the heating of the soil. As a consequence, the active layer thickens and the rate of decomposition increases which makes the soil more productive.

It has also been observed that many plants in the north are capable of withstanding fire. Black spruce has semi-serotinous cones and birch can reproduce vegetatively from stump sprouts. Most shrubs are capable of vegetative reproduction, by sprouting underground roots, stems, or rhizomes, which are found at various depths (Dyrness et al. 1986). After a fire, ruderal herbaceous species, such as *Epilobium angustifolium* L. (Fireweed) and *Calamagrostis canadensis* (Michx.) Beauv. (Bluejoint), quickly establish themselves in the burnt site.

1.4 Vegetation

The vegetation in the boreal region is a mosaic of forest, shrub, grassland, bog, and tundra types. Their distribution has been determined by slope, aspect, elevation, parent material, and succession after wildfire (Viereck et al. 1986). The boreal forests of North America are characterized primarily by slow-growing black spruce (*Picea mariana*) and white spruce (*Picea glauca*). Viereck et al. (1983) argue that these two species occupy different habitats and form two distinct forest types along a gradient of soil moisture and soil temperature in central Alaska. The forests on warm mesic sites - mainly south facing - are dominated by white spruce, whereas the cold and wet sites are dominated by black spruce. The black spruce sites are, in most cases, underlain by permafrost and often covered with moss. Deciduous trees are frequently seen after a fire, and these include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), and white birch (*Betula papyrifera*

Marsh.) (Kelsall 1977). Northward in the boreal forest region, dwarf birch (*Betula glandulosa* Michx.) and Labrador tea (*Ledum groenlandicum* Oeder) are quite common in bogs and upland forest (Kelsall 1977).

2. Kluane region

This research was conducted in the Kluane region, near Kluane Lake, in the southwest region of the Yukon Territories (Fig. 2). The Kluane region lies within the Shakwak Trench which runs along the western edge of the Yukon plateau (Fig. 3). The plateau lies between the St. Elias-Coast Mountains which rise abruptly from the Pacific Ocean and the interior Cassiar-Pelly Mountains (Fig. 3). Much of Yukon plateau, which occupies the southern area of the Yukon Territory, falls into the boreal forest biome.

The experimental site was about 1000 m above sea level and about 2 km south of "Mile 1049" on the Alaska Highway (Fig. 4). The site was set up close to the microwave tower.

2.1. Climate

The climate of the Yukon is sub-arctic continental. Criteria for a continental climate are large annual, day-to-day, and daily ranges in temperature, low to moderate moisture content, and moderate or light and irregular precipitation (Wahl et al. 1987).

At Burwash, 60 km to the northwest of the experimental sites, the annual mean temperature is below 0°C (Fig. 5). Changes in monthly mean temperature are also shown in
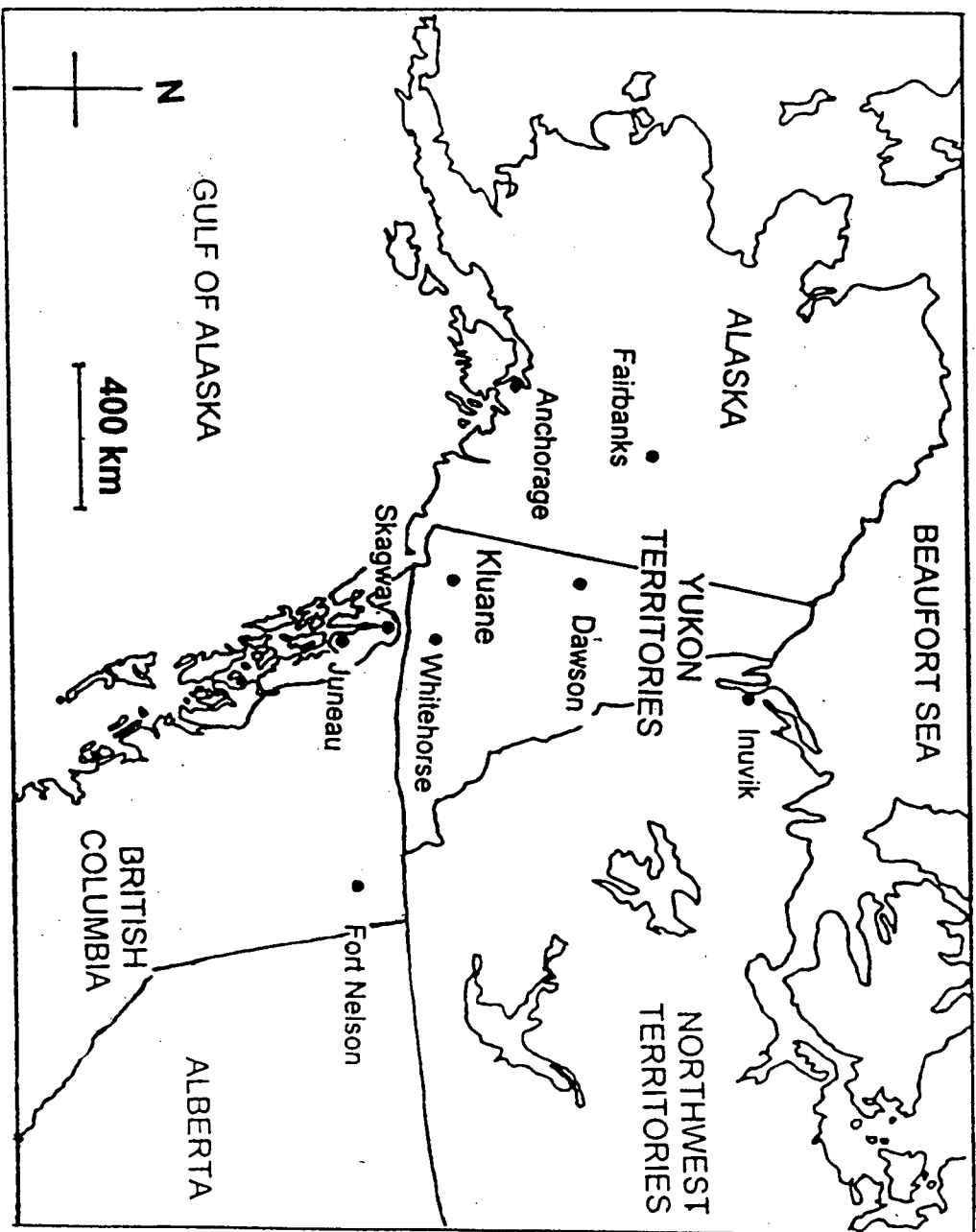
Fig. 2. Map of northwest Canada and Alaska.
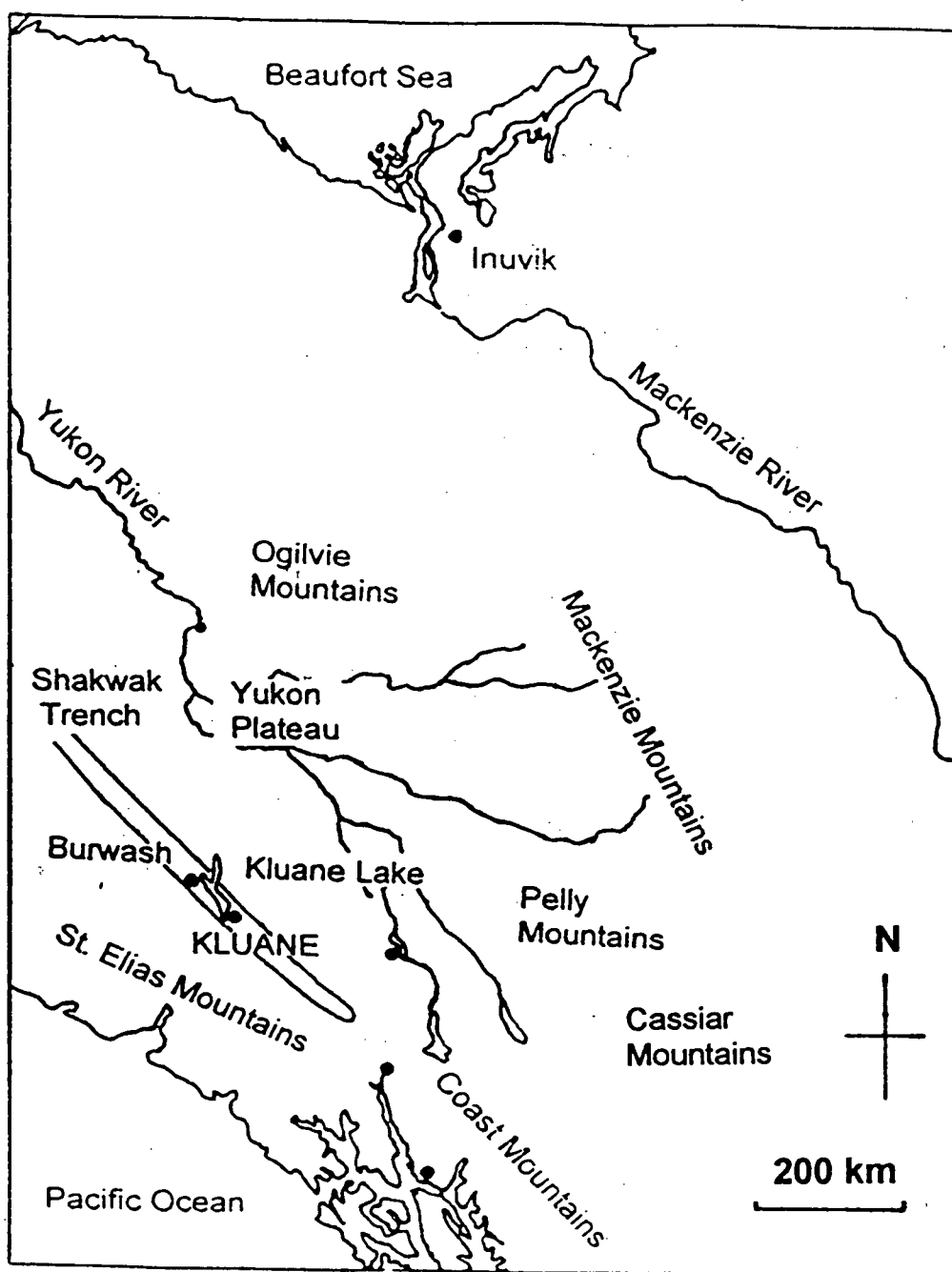
Fig. 3. Map of Yukon Territories, Canada.

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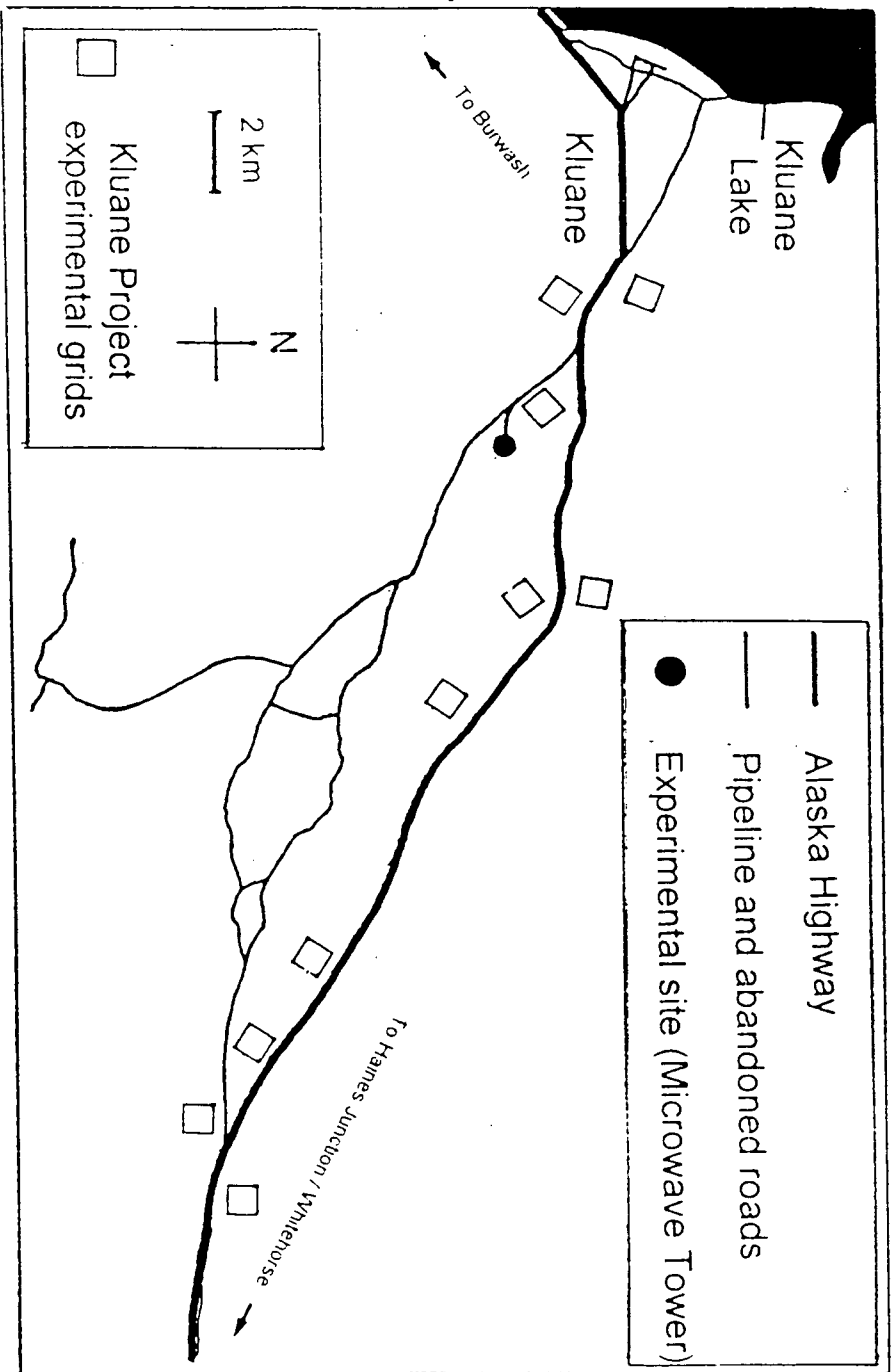
Fig. 4. Map of Kluane, Yukon Territories.
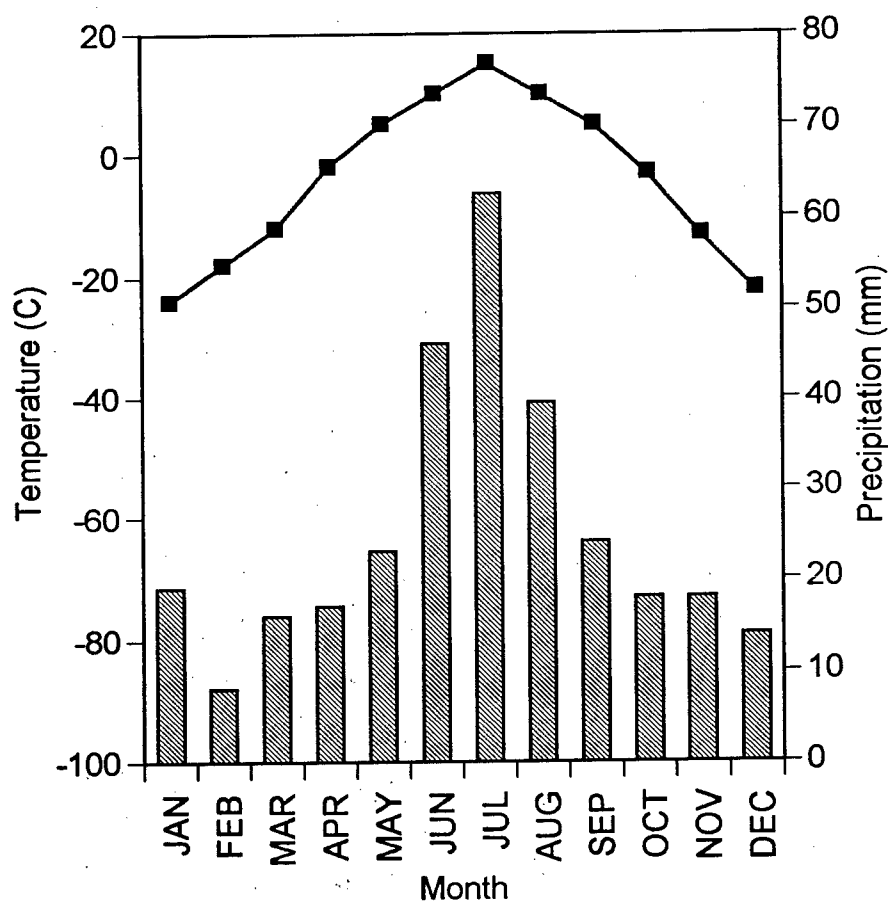
Fig. 5. Temperature and precipitation at Burwash, Yukon Territories. Line graph : monthly mean temperatures (1966 - 1980). Bar graph: monthly mean precipitation (1966 - 1980). (Data from Wahl et al. 1987)

Figure 5. The temperature regime is typically continental showing great variability on a daily basis as well as on a seasonal basis (Wahl et al. 1987). The average date of last frost and first frost at Kluane Lake is June 19 and August 18, respectively, giving a growing season of only 59-frost free days. The number of frost-free days at the experimental site is probably slightly fewer due to an elevation difference of nearly 300 m.

Much of the Yukon plateau receives 300 mm of precipitation annually and some localities receive only slightly more than 200 mm (Wahl et al. 1987) as it lies in the rain shadow of the St.Elias-Coast Mountains. Figure 5 shows changes in monthly mean precipitation at Burwash. The vicinity of Kluane Lake seems to be the most arid location within the Yukon plateau (Wahl et al. 1987).

2.2. Vegetation and soil characteristics

Forest covers most parts of the Yukon plateau up to elevations of 1300 m on south facing slopes and 600 m on north-facing slopes (Wahl et al. 1987). The vegetation around the experimental site falls into what Viereck et al. (1986) categorize as 'upland mesic white spruce'. The dominant tree in this region is mature white spruce (*Picea glauca*) with occasional stands of aspen (*Populus tremuloides*) and balsam popular (*Populus balsamifera*), with an understory containing dwarf birch (*Betula glandulosa*) and species of willow (*Salix spp.*), and a number of common herbaceous species including yarrow (*Achillea millefolium* L.), northern anemone (*Anemone parviflora* Michx.), altai fescue (*Festuca altaica* Trin.), arctic lupine (*Lupinus arcticus* S.Wats), and bluebells (*Mertensia paniculata* (Ait.) G.Don).

Soil characteristics are relatively consistent with what has been described in the previous section; low soil temperature, high moisture content, podzolization, and accumulation of litter. The nutrient availability in the mineral soil is very low.

2.3. Fire

In the Kluane region, fire is also a important part of the boreal forest dynamics. Close to the experimental site, a major fire occurred in 1872 which cleared a part of the forest and formed a meadow which gave rise to young trees (Shawn Francis, personal communication). Another small fire occurred in 1936 which burned a part of the meadow but did not extend to the forested area. The experimental site was at this edge of this forest.

B. Materials and methods

1. The species

Within the understory community, five common perennial herbaceous species were selected as "target species"; *Achillea millefolium* (yarrow), *Anemone parviflora* (northern anemone), *Festuca altaica* (altai fescue), *Lupinus arcticus* (arctic lupine), and *Mertensia paniculata* (bluebells). Descriptions of their morphology and distributions are found in Hultén (1968), Hitchcock and Cronquist (1973), Anderson and Welsh (1974), Trelawny (1988), and Mackinnon et al. (1992).

2. Experimental design

At the end of May 1994, an area within the boreal forest understory, approximately 50 m x 50 m, provided adequate sites to accommodate all of the experimental plots. Experimental plots were only established in sites which satisfied the following three conditions: 1) relatively open patches within the forest where light penetrates to ground level, 2) all of the five target species are present in the patch, 3) almost a complete absence of a moss layer.

Thirty-six emerging shoots of each target species were randomly located within the understory community. A 50 cm x 50 cm plot was centered over each target individual. For every target species, there were three competition treatments; I- (isolated), C- (coned), and N- (natural) treatments (Table 1). The purpose of the three competition treatments was to measure the total competition intensity and also to divide it into below- and aboveground components. To accomplish this, a method used by Belcher et al. (1995) was adopted. Chicken wire cones, with a mesh size of 2.5 cm, were made and placed around each of the target individuals (Fig. 6). In the C-treatment, the shoots of neighboring individuals were made to grow outside of the cone enabling sunlight to penetrate to ground level inside the cone. This reduces aboveground competition for the target individuals. In the N-treatment, the shoots of neighboring individuals were allowed to grow through the chicken wire cone, thus having both aboveground and belowground competition. This treatment serves as the control because it is identical to natural conditions except for the presence of the cone surrounding the target individual. In the I-treatment, all surrounding vegetation within the plots were removed (aboveground only), but cones were still placed to control for the presence of the chicken wire in the other treatments.

Table 1. Definitions of each treatment and its abbreviation.

Abbreviations	Treatments
I	**_Isolated_** No competition occurring. All plants surrounding the target individual removed.
C	**_Coned_** Only belowground competition occurring. Plants surrounding the target individual were not removed. However, the target individual is surrounded by cone-shaped chicken-wire to displace the aboveground parts of neighbors away from the target individual.
N	**_Natural vegetation_ (control)** Competition occurring both above- and belowground. No treatment.
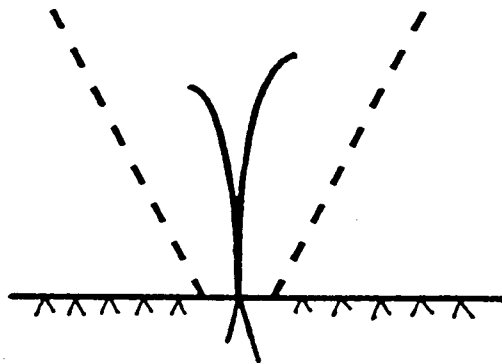
Isolated (I)

no competition
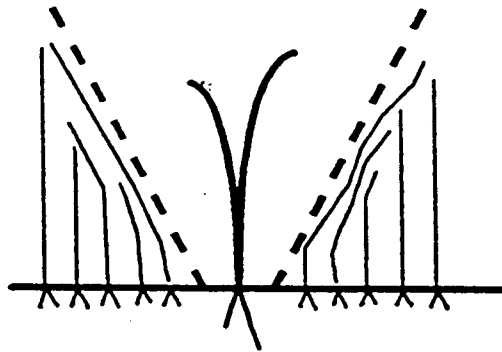
Coned (C)

belowground
competition
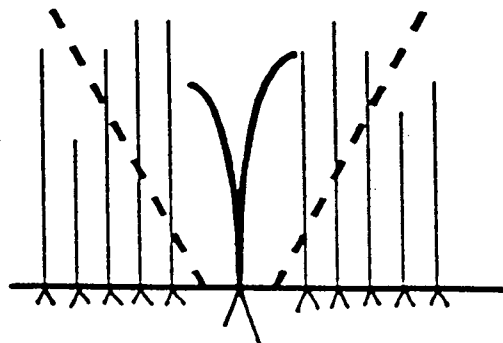
Natural (N)

above- and
belowground
competition

Figure 6. Diagram of competition treatments; I, C, N. For further details see Table 1.

Each of the three competition treatments was factored by three fertility levels; low, medium, and high. Low fertility plots were not fertilized and served as a control. Medium and high fertility treatments were imposed by applying fertilizer[4] at 200 g/m^2 and 400 g/m^2, respectively. Thus, the design of the experiment was a 3x3 factorial with four replicates for each species.

Both competition and fertility treatments were set up during May 27-30, 1994. Fertilization took place three more times during the growing season (June 18, July 7, July 20). Quadrats were maintained each week making sure that treatments were continuously imposed on the target individuals (i.e. keeping shoots of plants apart, and removing regrowing neighbors). At the time of the initial setup, measurements of the target individuals (Table 2) were made which were later used as a covariate for analysis of covariance (ANCOVA). The measurements made were good estimators for initial individual biomass (Appendix 1). During the experimental period, target individuals that flowered were recorded.

All the target individuals were harvested within the period of August 2 - 5. Leaf number at harvest was counted for the target individuals, which were then oven dried at 40°C for at least 10 days, and weighed. At the same time, leaf area index (LAI) was measured on nine sampling points within each plot of the C- and N-treatment plots. Then the surrounding vegetation within the plot was also harvested, oven dried at 40°C for at least 10 days, and weighed.

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[4] Fertilizer added was a water-soluable quick release as 6:8:6 (NPK).

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Table 2. Measurements used as covariates for each species.

Species	Measurements
Anemone parviflora	Width of leaf (cm)
Achillea millefolium	Number of leaves
Festuca altaica	Clump diameter (cm)
Lupinus arcticus	Clump diameter (cm)
Mertensia paniculata	Length of longest leaf (cm)

3. Statistical analysis

3.1. Flowering response in Achillea millefolium and Mertensia paniculata

All target individuals of *A. parviflora*, *F. altaica*, and *L. arcticus* flowered, but not all the target individuals of *A. millefolium* and *M. paniculata* did so. Both *A. millefolium* and *M. paniculata* have a rosette growth form during vegetative growth and form flower shoots to reproduce. The result of this may be great differences in biomass and leaf number at the time of harvest. Chi-square analysis was done to determine if flowering occurred in response to fertilizer treatment. Also, t-tests were done to test if there were any significant differences in biomass and leaf number between flowering and non-flowering individuals.

3.2. Treatment differences

Analyses of covariance (ANCOVA) were done separately for each species using SYSTAT MGLH (Wilkinson et al. 1992) to examine the effect of fertilizer and competition treatments on biomass and leaf number at harvest. Covariates are listed in Table 2. In all cases before ANCOVA were done, data were tested for homogeneity of regression. To improve the reliability of the test, all of the original data were $\log_e$ transformed to stabilize the variance among the treatments and to obtain near normal distribution. A few outliers were removed as determined by SYSTAT MGLH and SYSTAT GRAPH. To assess the effect of different treatments, adjusted least square means (log value) were obtained from ANCOVA and, if necessary, were subsequently followed by Fisher's Least Significant Difference test for pairwise comparisons.

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3.3. Surrounding vegetation

In this study 'surrounding vegetation' will be referred to as the vegetation surrounding the target individual within each plot. Leaf area index (LAI) of surrounding vegetation was estimated to ensure that the biotic environment (= mass and species composition of neighbors) did not differ significantly among the plots.

Using the leaf area index obtained from each plot (summed value of nine sampling points in each plot), analysis of variance (ANOVA) was done to determine the effects of fertility and competition treatments and also to detect if there will be differences in surrounding vegetation depending on the target species. The target species effect was included in the analyses because the vegetation surrounding different target species may differ significantly. The analysis was done using SYSTAT ANOVA. A regression analysis was done between leaf area index (LAI) and total biomass of surrounding vegetation.

Also using leaf area index data, principal components analyses (PCA) were done to determine the extent of differences in species composition among the plots.

4. Calculations of indices

4.1. Calculation of competition intensity (CI)

The intensity of competition was calculated as a relative reduction in biomass between the treatments (Grace 1993). For each fertility level of each species, total, root, and shoot competition intensity indices (CI) were calculated using the following equations:

$$\text{Total competition (TC)}^5 = (I - N) / I \qquad [1]$$

$$\text{Root competition (RC)} = (I - C) / I \qquad [2]$$

$$\text{Shoot competition (SC)} = (C - N) / I \qquad [3]$$

The abbreviations, I, C, and N, refer to the adjusted mean of each competition treatment. Competition intensity indices were calculated using biomass and leaf number separately.

Competition intensity is calculated as a value relative to the I-treatments. This was done to make among-species comparisons. For example, a reduction of 1 g caused by competition (difference between I-treatment and N-treatment) may not be important for an individual that weighs 100 g while it may be extremely important for an individual that weighs 10 g. Therefore, competition intensity is calculated as the absolute reduction of biomass relative to the mean biomass of a plant growing in isolation. This enables us to compare the relative importance of competition among species.

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[5] Total competition (TC) = Root competition (RC) + Shoot competition (SC)

4.2. Calculation of reduction relative to maximum growth

In this calculation, the adjusted mean of the isolated treatment with high fertility was considered as the maximum potential growth a target species may attain (abbreviated as M). The objective of this calculation was to determine the relative importance of fertility and competition to total reduction in a natural habitat (= low fertility). The indices were calculated as :

$$\text{Total reduction } (RT)^6 = (M - N) / M \qquad [\,4\,]$$

$$\text{Reduction by fertility } (RF) = (M - I) / M \qquad [\,5\,]$$

$$\text{Reduction by competition } (RC) = (I - N) / M \qquad [\,6\,]$$

where, I: adjusted mean of the I-treatment, N: adjusted mean of the N-treatment. This index was calculated for biomass only.

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[6] Total reduction (RT) = Reduction by fertility (RF) + Reduction by competition (RC)

Chapter 3. Results

A. Flowering of Achillea millefolium and Mertensia paniculata

Chi-square analysis showed the occurrence of flowering to be independent of fertility treatments for *A. millefolium* (Table 3a). In a t-test between flowering and non-flowering individuals, significant differences in both biomass ($P = 0.008$) and leaf number ($P < 0.001$) were detected. For *M. paniculata*, chi-square analysis again showed that flowering occurred independent of fertility treatments (Table 3b). T-tests showed no significant difference in biomass between the flowering and non-flowering individuals ($P = 0.849$), but detected a significant difference in leaf number ($P < 0.001$).

Results for both species show that flowering is not influenced by fertility treatment. However, once individuals flower, they may skew the results of ANCOVA performed on the target individuals because of the significant increases in biomass and leaf number for *A. millefolium*. Therefore, in the next section where ANCOVA was used to test for significant differences among the treatment means, two sets of analyses were done for *A. millefolium* and *M. paniculata*; the first done on all individuals and the second done with flowering individuals excluded.

Table 3. Results of chi-square analysis on flowering of *Achillea millefolium* and *Mertensia paniculata*. a) *Achillea millefolium* b) *Mertensia paniculata*.

a)

H_0 : Flowering is not dependent on fertility level.
H_A : Flowering is dependent on fertility level.

	Fertility levels		
	Low	Medium	High
No. of flowering individual	2	1	3
No. of non-flowering individual	10	11	9

Result of calculation: $\chi^2 = 1.2$, DF = 2
Critical value ($P=0.05$): $\chi^2_{0.05, 2} = 5.991$

Thus, do not reject H_0.

b)

H_0 : Flowering is not dependent on fertility level.
H_A : Flowering is dependent on fertility level.

	Fertility levels		
	Low	Medium	High
No. of flowering individual	1	2	3
No. of non-flowering individual	11	10	9

Result of calculation: $\chi^2 = 1.2$, DF = 2
Critical value ($P=0.05$): $\chi^2_{0.05, 2} = 5.991$

Thus, do not reject H_0.

B. Responses to treatments

1. Statistical considerations

None of the ANCOVA tests presented here had significant interactions between treatments and covariates, thus satisfying the assumption of homogeneity of regression. Due to the removal of a few outliers, sample sizes became unequal, but SYSTAT adjusts for this problem (Tabachnick and Fidell 1989). It is noteworthy that in the case of *A. millefolium* and *M. paniculata*, where the analyses were done with the flowering individuals excluded, some treatments had sample size as low as 2. Complete ANCOVA tables of all analysis are shown in Appendix 2.

2. Responses to fertilizer treatment

In this section, target individuals of each species are grouped by fertility treatments and summed across all competition treatments; thus each fertility level should have a sample size of 12 unless outliers or flowering individuals were removed. An adjusted mean (log-value) for each fertility level was obtained using SYSTAT (Wilkinson et al. 1992).

Anemone parviflora

Fertilizer had a strong effect on survivorship. There was 100% survival of target individuals in the low fertility treatment, but successively higher mortality with increasing fertility with nearly 80% of individuals dying in the highest fertility (Fig. 7). At medium fertility, about

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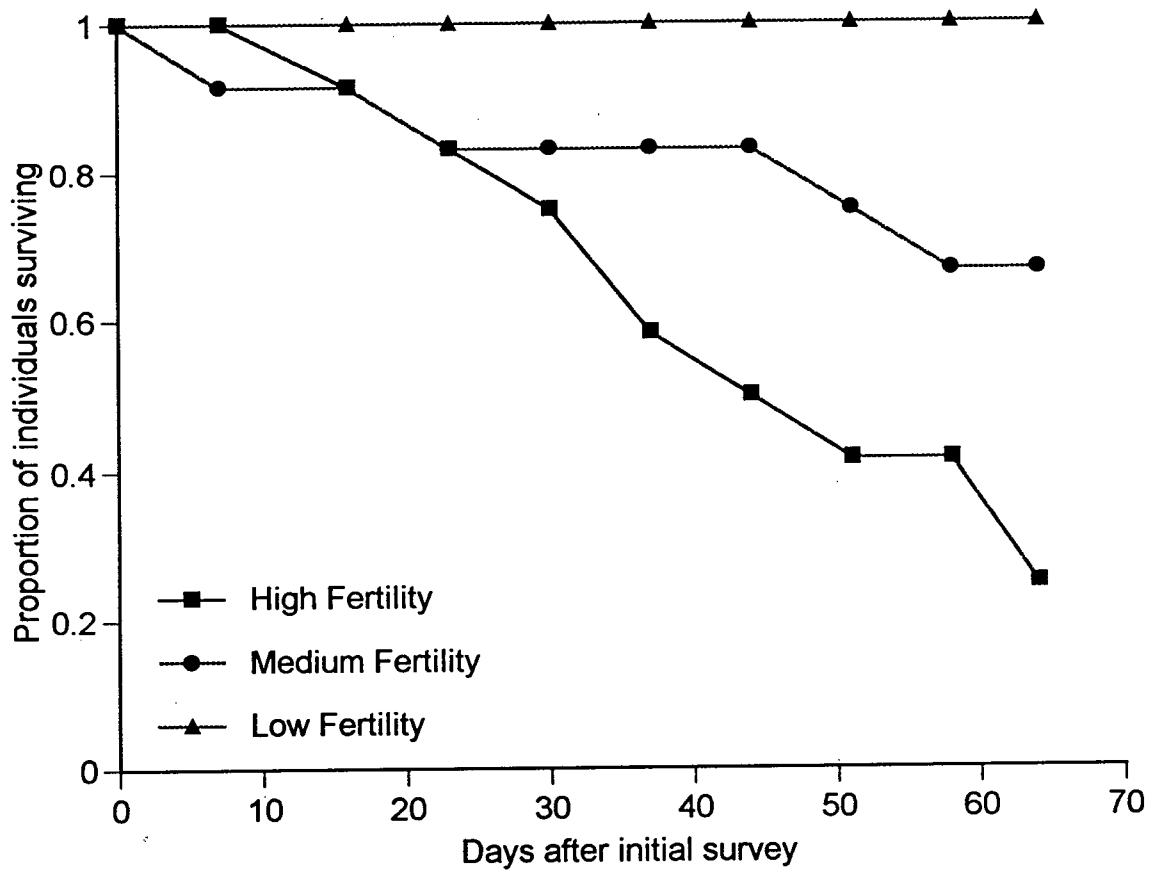
Fig. 7. Survivorship curves for populations of *Anemone parviflora* growing at three different fertility levels. The initial survey was done on May 30, 1994.

40% died before the end of the growing season. The logrank test (Hutchings et al. 1991) detected a significant difference in mortality between the unfertilized and fertilized treatments, indicating that *A. parviflora* cannot tolerate the increased nutrient availability.

Achillea millefolium

Achillea millefolium responds positively to the addition of fertilizer. Regardless of whether flowering individuals were included in the data set or not, both biomass (Fig. 8a, 10a) and leaf number (Fig. 9a, 11a) increased significantly (Table 4a). However, differences in both biomass and leaf number were not statistically significant between medium and high fertility treatments when flowering individuals were excluded.

Festuca altaica

Festuca altaica also responded positively to fertilizer addition. Both biomass (Fig. 12a) and leaf number (Fig. 13a) increased with increasing fertility (Table 4a). However, the difference between medium and high fertility was not significant for either variable.

Lupinus arcticus

There were no changes in biomass with increasing fertility levels (Fig. 14a). Leaf number tended to decrease with higher fertility (Fig. 15a) although it was not significantly different (Table 4a).

Mertensia paniculata

There were nonsignificant increases in both biomass (Fig. 16a) and leaf number (Fig. 17a) with increasing fertility level (Table 4a). Nonsignificant increases were also obtained when the flowering individuals were excluded from the data set for both biomass and leaf number (Fig. 18a, 19a).

3. Responses to competition treatments

In this section, target individuals of each species are grouped by competition treatments and summed across all fertility treatments; thus each competition level should have sample size of 12 unless outliers or flowering individuals are removed. An adjusted mean (log-value) for each competition treatment was obtained using SYSTAT (Wilkinson et al. 1992).

Anemone parviflora

Due to high mortality in the fertilized plots, the effects of the competition treatments were investigated using low fertility data only (each competition treatment: n = 4). ANOVA was used instead of ANCOVA due to nonsignificance of the covariate. Both biomass (Fig. 20a) and leaf number (Fig. 20b) showed a nonsignificant decreasing trend with increasing influence of neighbors, i.e. from isolated individuals (I-treatment), through the C-treatment (neighbors present but shoots deflected away from the target individual), to the N-treatment (control) (Table 4b).

Achillea millefolium

There was a decrease in biomass with increasing influence of neighbors (Fig. 8b, 10b), but significant differences were found only when the flowering individuals were included in the analysis (Table 4b). Significant decrease from I- to C-treatment were found in leaf number with or without the flowering individuals in the analysis (Fig. 9b, Fig. 11b).

Festuca altaica

Biomass decreased with higher intensity of competition (Fig. 12b) although it was not significant (Table 4b). Leaf number decreased significantly from I- to C-treatment (Fig. 13b) indicating belowground competition. There was a nonsignificant increase in leaf number from C- to N-treatment (= aboveground competition) (Fig. 13b).

Lupinus arcticus

Neither biomass (Fig. 14b) nor leaf number (Fig. 15b) showed any response to the competition treatment (Table 4b).

Mertensia paniculata

Biomass did not show any response to competition treatments with (Fig. 16b) or without (Fig. 18b) flowering individuals included in the analyses (Table 4b). Same results were also obtained for leaf number (Fig. 17b, 19b).

4. Responses to competition treatments with increasing fertility

In this section, the combined effects of the fertility treatments and competition treatments are examined to investigate the species responses to competition treatments with increasing fertility. Sample size in each treatments is 4.

Anemone parviflora

Due to high mortality in the fertilized plots, it was not possible to assess differences in biomass and leaf number caused by competition treatments along a gradient of increasing fertility.

Achillea millefolium

In both analyses with and without the flowering individuals (Fig. 8c, 10c), comparison of biomass at low fertility shows no effect of the competition treatments. However, at medium fertility, a decrease in biomass from I- to C-treatment is apparent. At high fertility, decrease in biomass from C- to N-treatment becomes apparent, although statistically nonsignificant.

In both analyses with and without flowering individuals (Fig. 9c, 11c), leaf number at low fertility shows a unique pattern with C-treatment having the smallest mean value, although the differences are not significant. At medium fertility, the pattern is identical to the results of biomass, where belowground competition has a significant effect.

Festuca altaica

Biomass of *F. altaica* at low fertility shows no differences among competition treatments, but as fertility increases, a difference appears between I- and N-treatment (= total competition). However, none of the differences is significant at any fertility level (Fig. 12c).

Leaf number did not show significant differences among the competition treatments at any of the fertility levels (Fig. 13c). However, at medium and high fertility, there is a slight decrease from I- to C-treatment.

Lupinus arcticus

No significant differences or trends were found between competition treatments for both biomass and leaf number at any fertility level (Fig. 14c, 15c).

Mertensia paniculata

With or without the flowering individuals included in the analyses, no significant differences were found between competition treatments for both biomass and leaf number at any fertility level (Fig. 16c, 17c, 18c, 19c).

Table 4. Summary of analysis of covariance. a) Fertilizer treatment b) Competition treatment. No significant interactions were found in any of the analyses. Analyses were based on log-transformed data for both biomass and number of leaves. Bold indicates $P <$ 0.05. Details of each analysis are shown in Appeddix 2.

a) Fertilizer treatment

Species	Variable	Flowering individuals included (P)	Flowering individuals excluded (P)
Anemone parviflora [1]	biomass	N/A	N/A
	leaf number	N/A	N/A
Achillea millefolium	biomass	**<0.001**	**<0.001**
	leaf number	**<0.001**	**0.008**
Festuca altaica	biomass	**<0.001**	N/A
	leaf number	**<0.001**	N/A
Lupinus arcticus	biomass	0.997	N/A
	leaf number	0.086	N/A
Mertensia paniculata	biomass	0.406	0.738
	leaf number	0.614	0.993

[1] Due to high mortality in the fertilized plots analysis of covariance was not done.

b) Competition treatment

Species	Variable	Flowering individuals included (P)	Flowering individuals excluded (P)
Anemone parviflora [2]	biomass	0.269	N/A
	leaf number	0.355	N/A
Achillea millefolium	biomass	**0.048**	0.208
	leaf number	**0.032**	**0.05**
Festuca altaica	biomass	0.295	N/A
	leaf number	**0.035**	N/A
Lupinus arcticus	biomass	0.943	N/A
	leaf number	0.271	N/A
Mertensia paniculata	biomass	0.199	0.379
	leaf number	0.995	0.555

[2] Due to high mortality in the fertilized plots, analysis was done with only low fertility level data. And due to the nonsignificance of the covariate, analysis of variance was done.
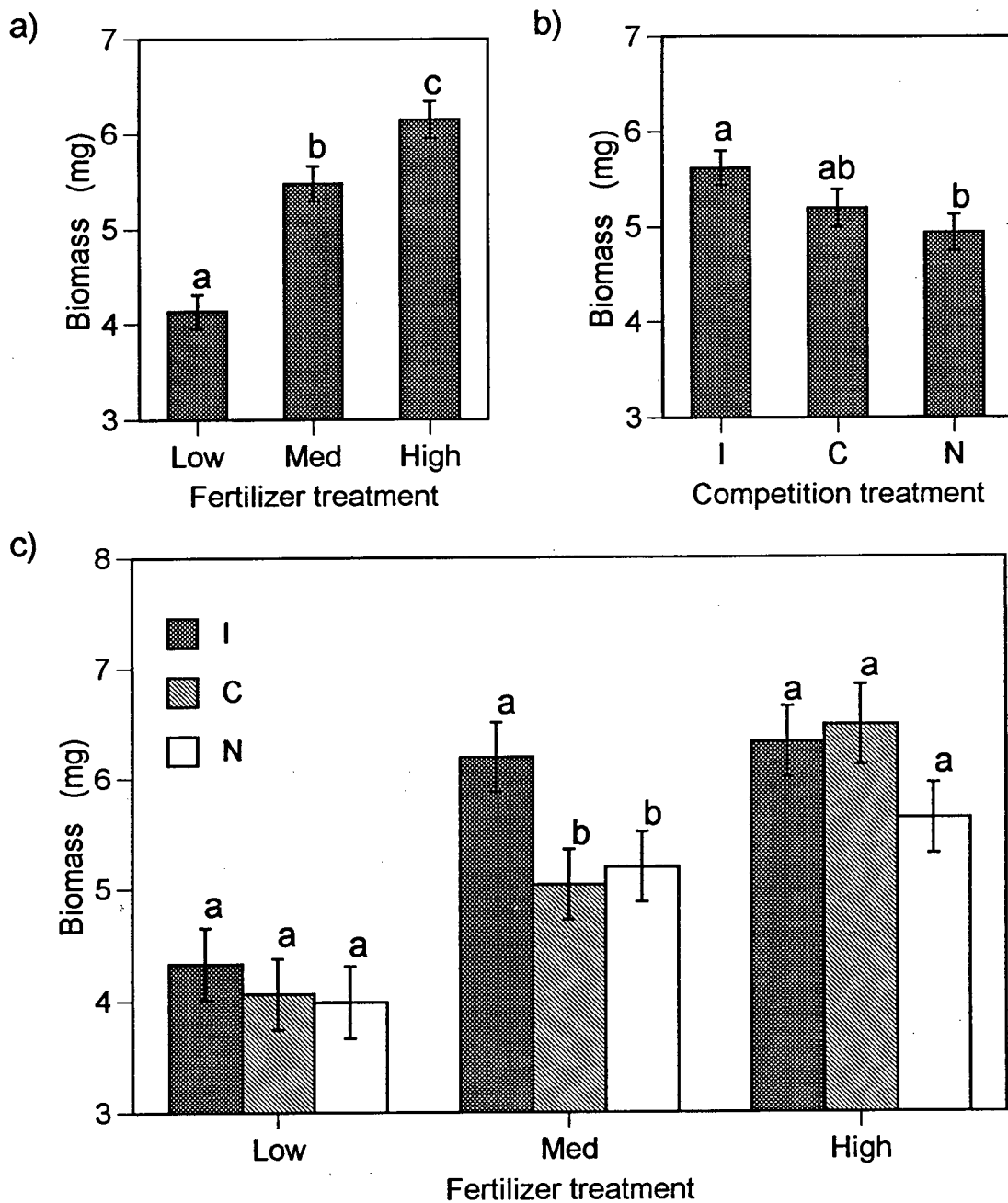
Fig. 8. Mean biomass (and S.E.) of *Achillea millefolium* (with flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
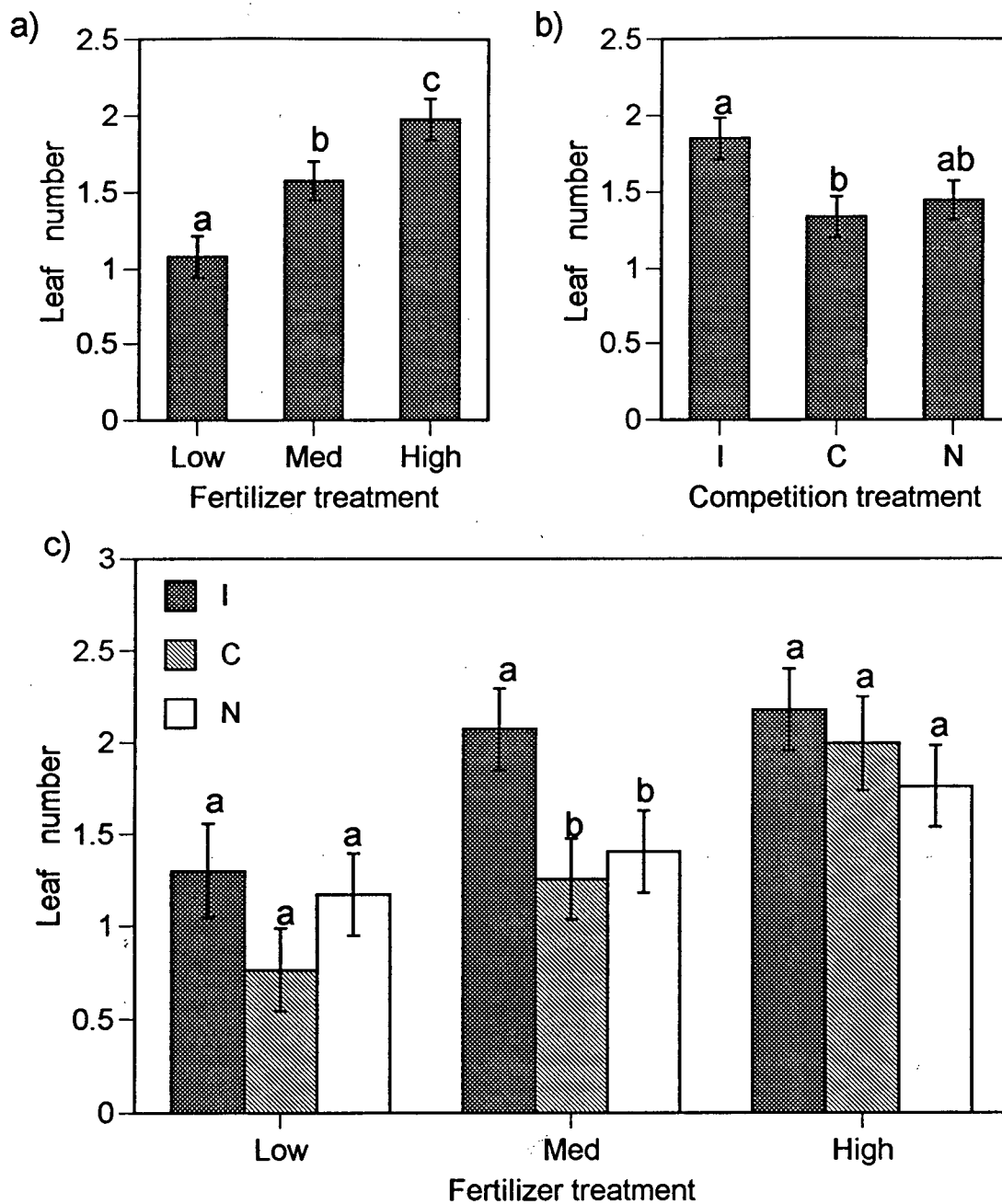
Fig. 9. Mean number of leaves (and S.E.) of *Achillea millefolium* (with flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
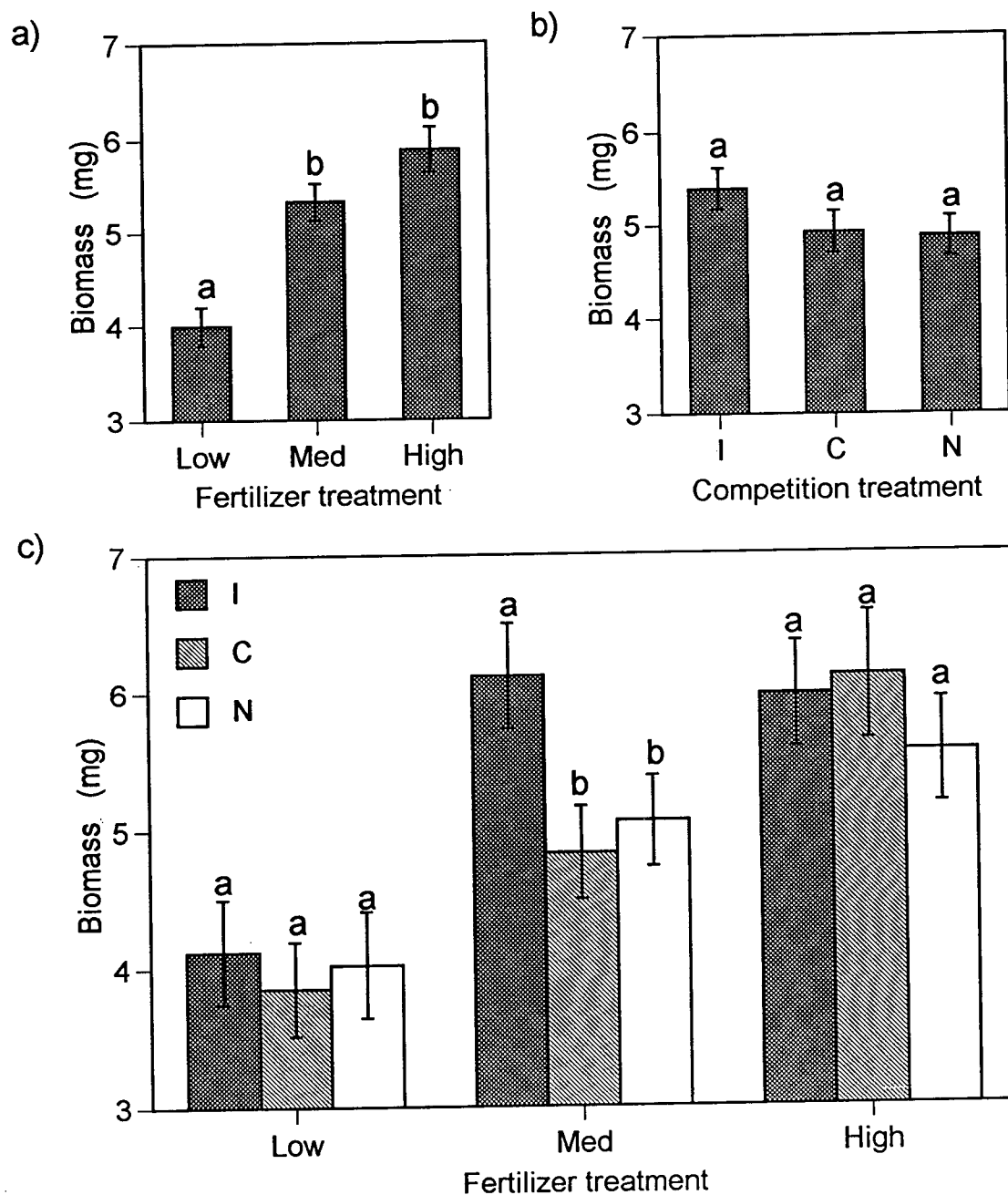
Fig. 10. Mean biomass (and S.E.) of *Achillea millefolium* (without flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
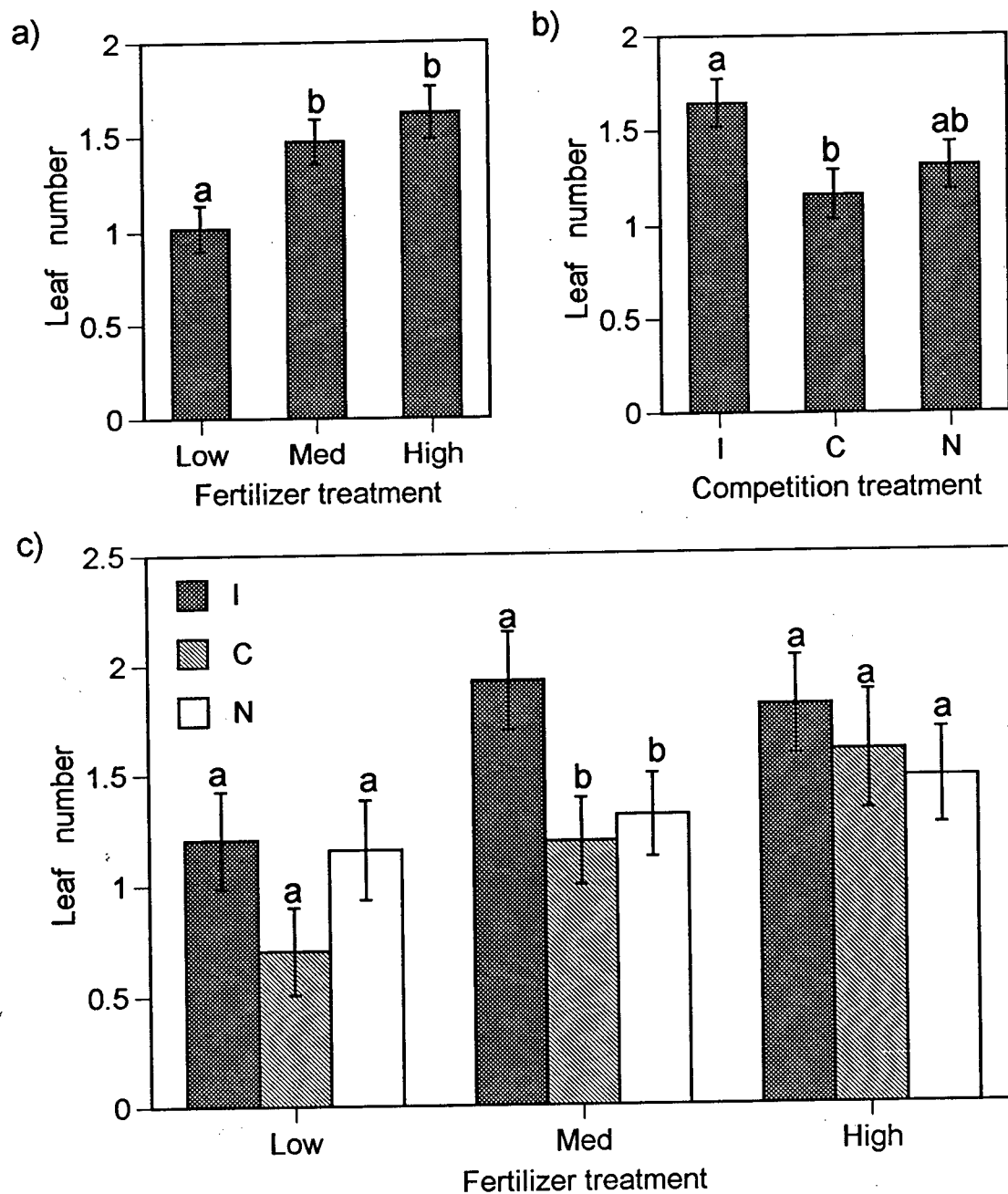
Fig. 11. Mean number of leaves (and S.E.) of *Achillea millefolium* (without flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), colums sharing the same letter are not significantly different (*P* > 0.05; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different (*P* > 0.05; LSD).

Fig. 12. Mean biomass (and S.E.) of *Festuca altaica* by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).

Fig. 13. Mean number of leaves (and S.E.) of *Festuca altaica* by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
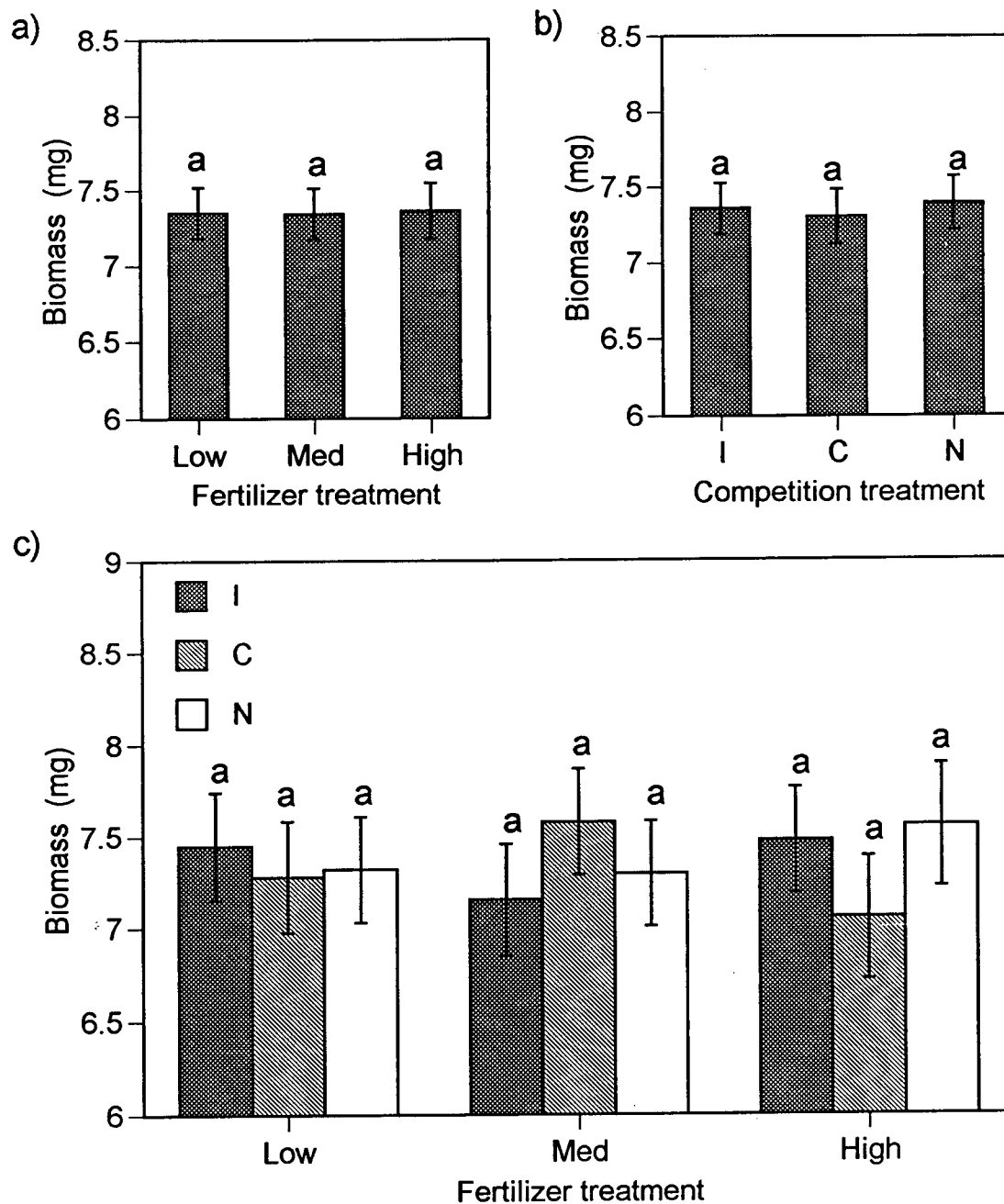
Fig. 14. Mean biomass (and S.E.) of *Lupinus arcticus* by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different (*P* > 0.05; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different (*P* > 0.05; LSD).
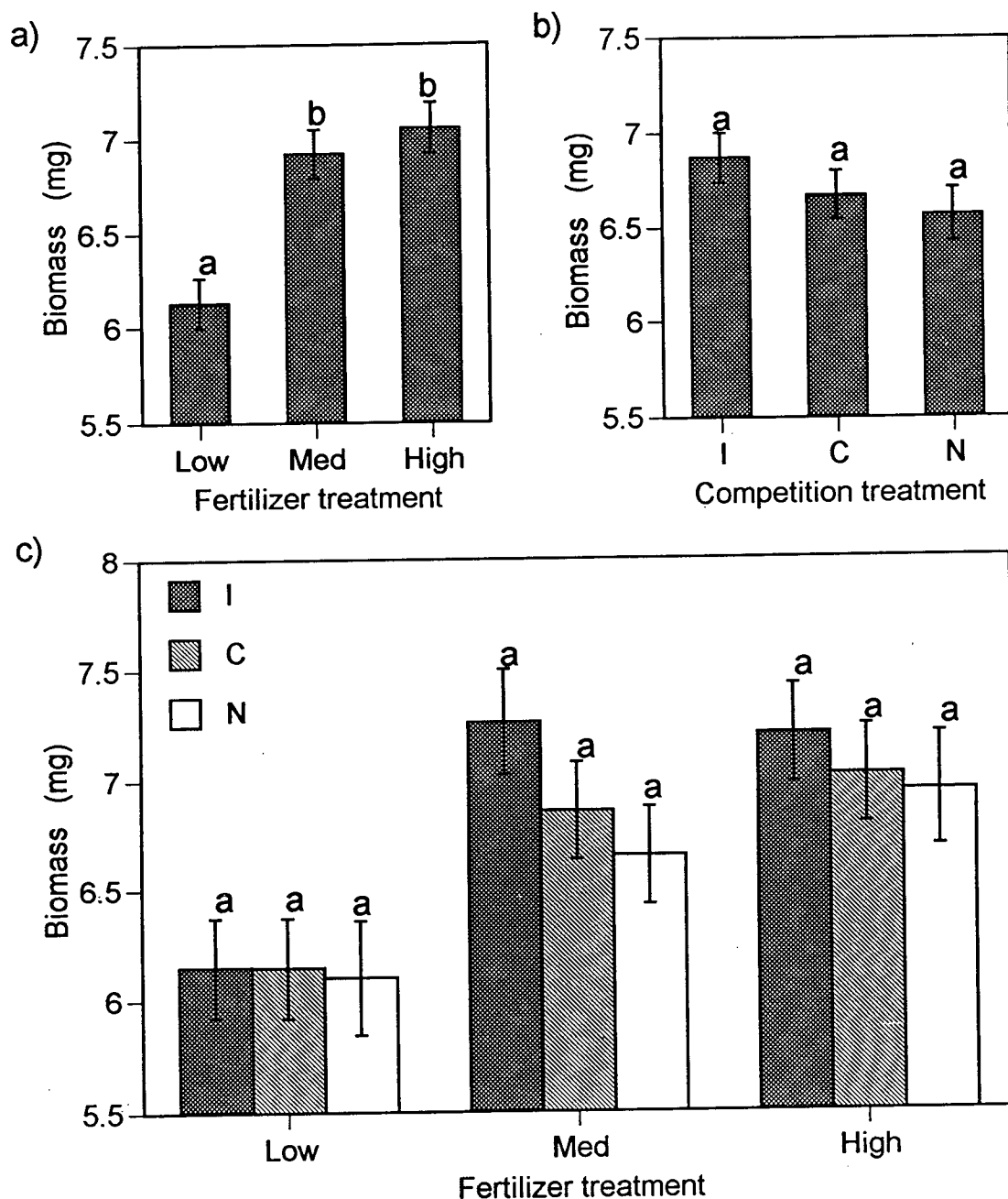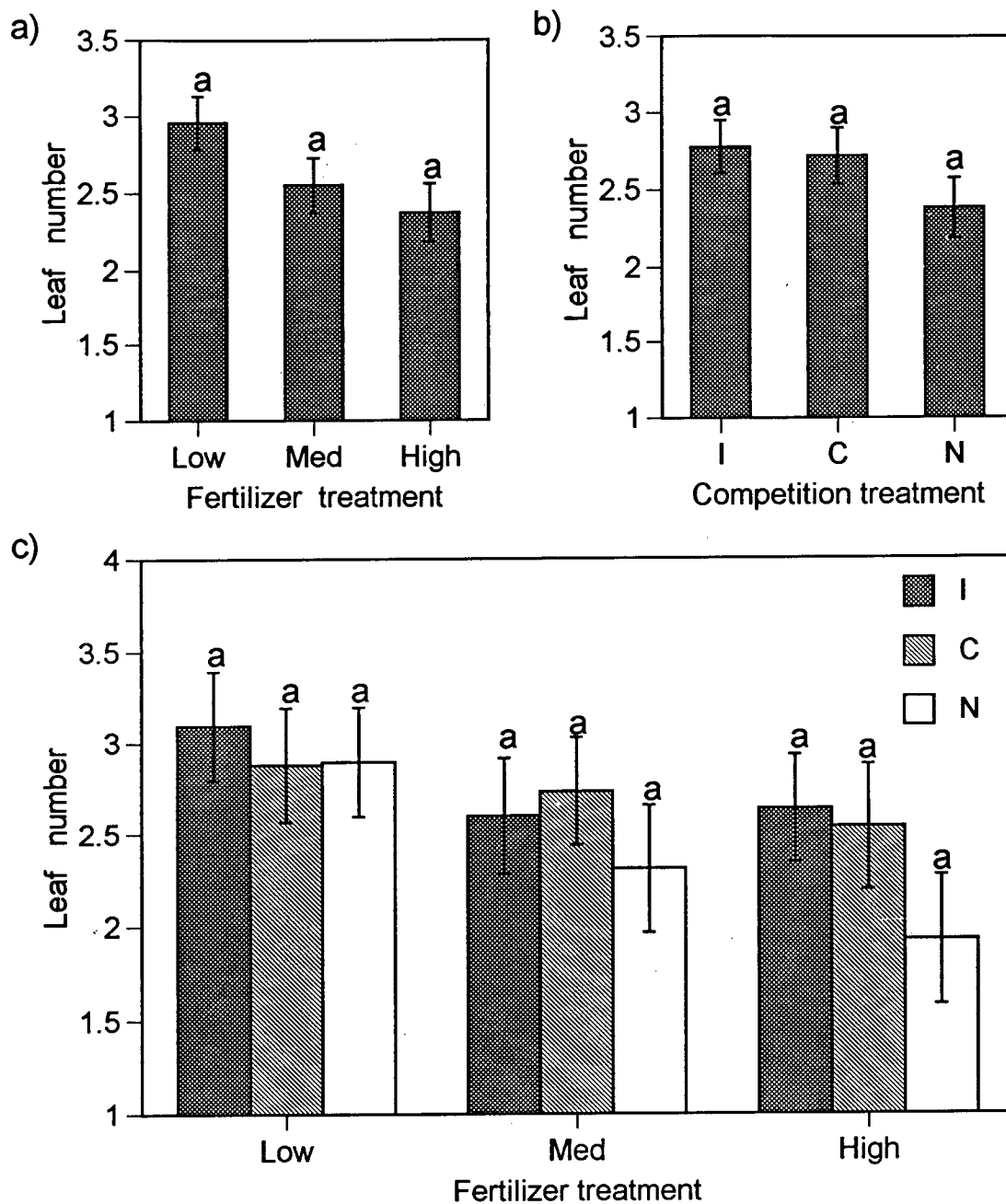
Fig. 15. Mean number of leaves (and S.E.) of *Lupinus arcticus* by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
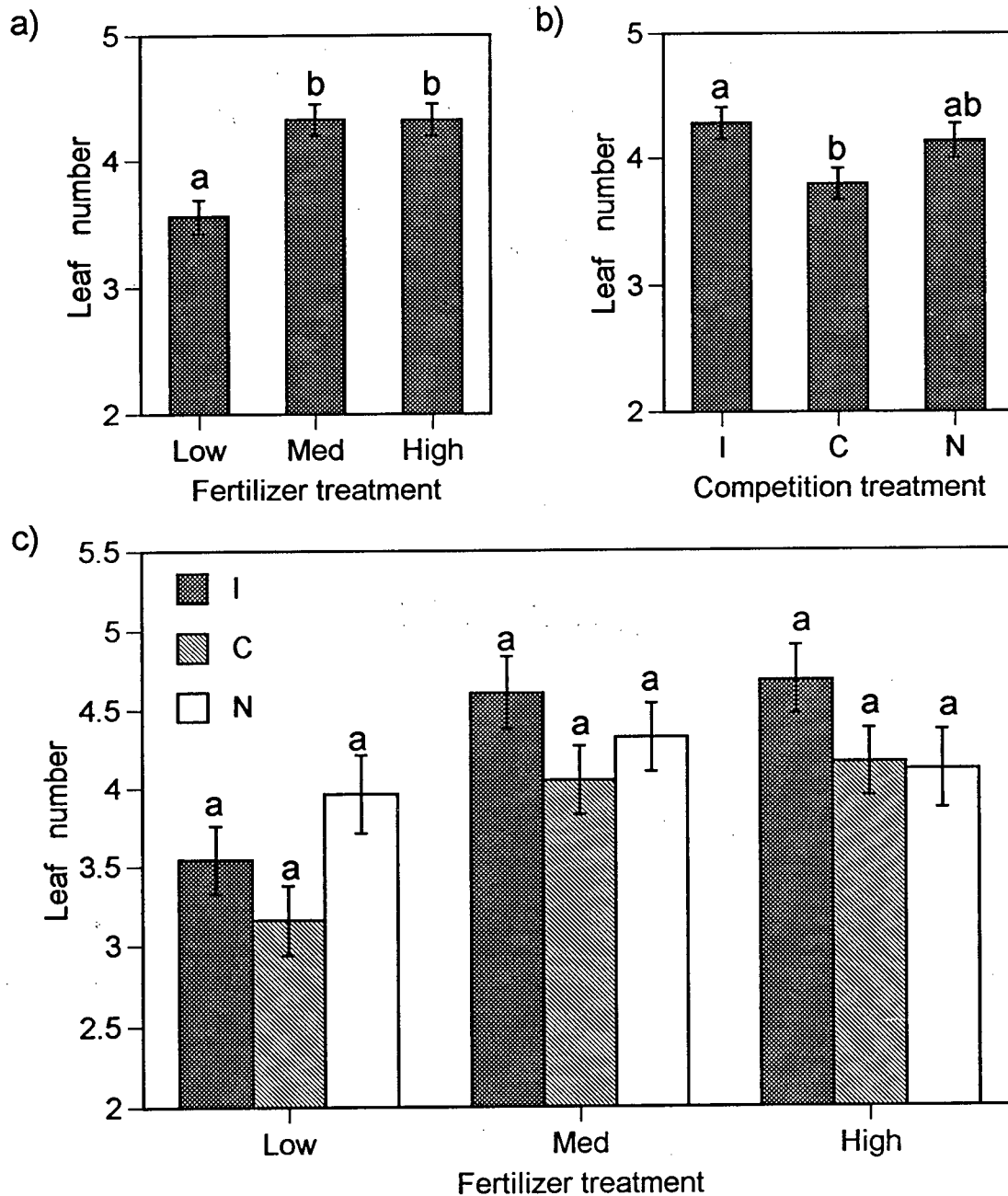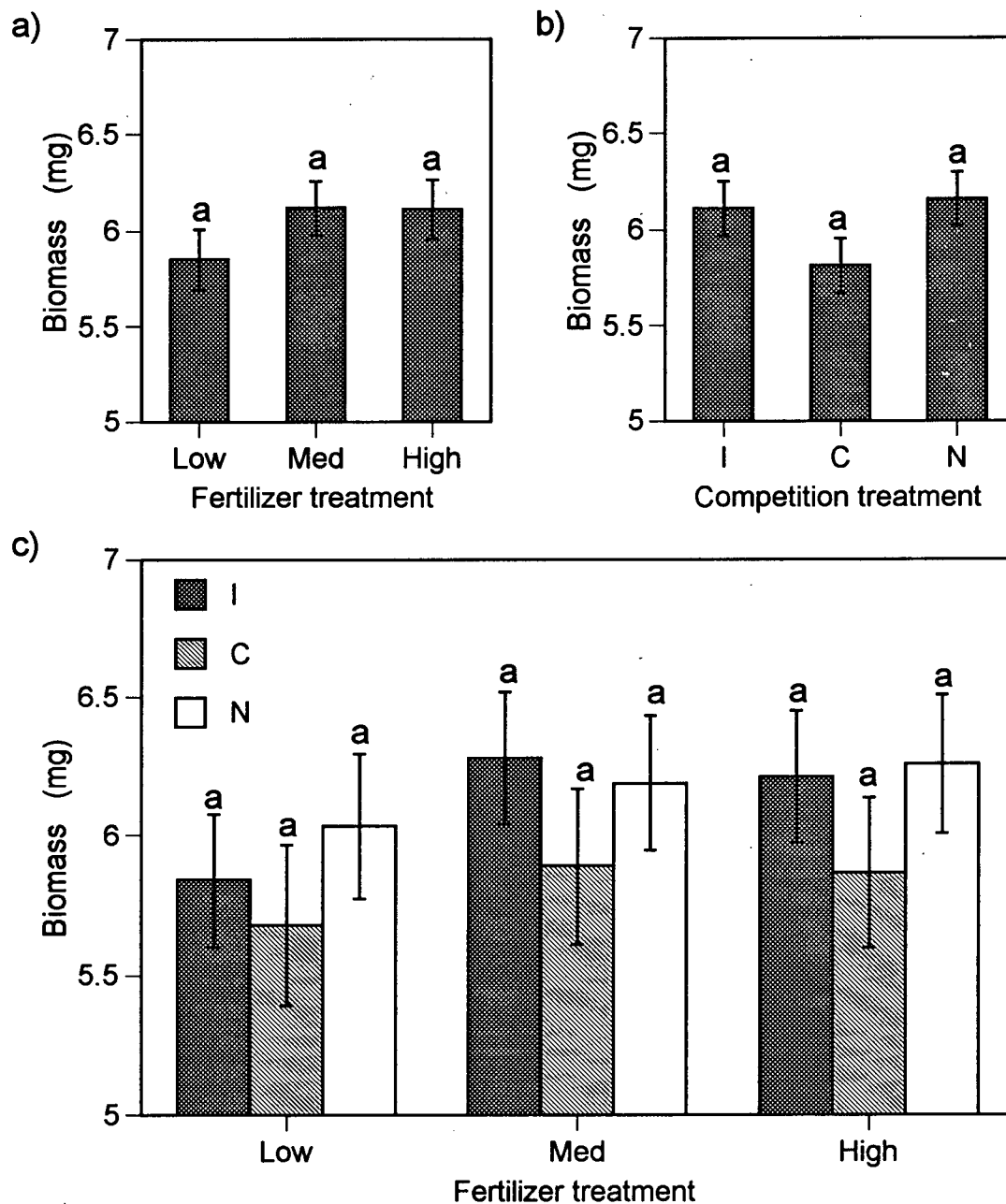
Fig. 16. Mean biomass (and S.E.) of *Mertensia paniculata* (with flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).
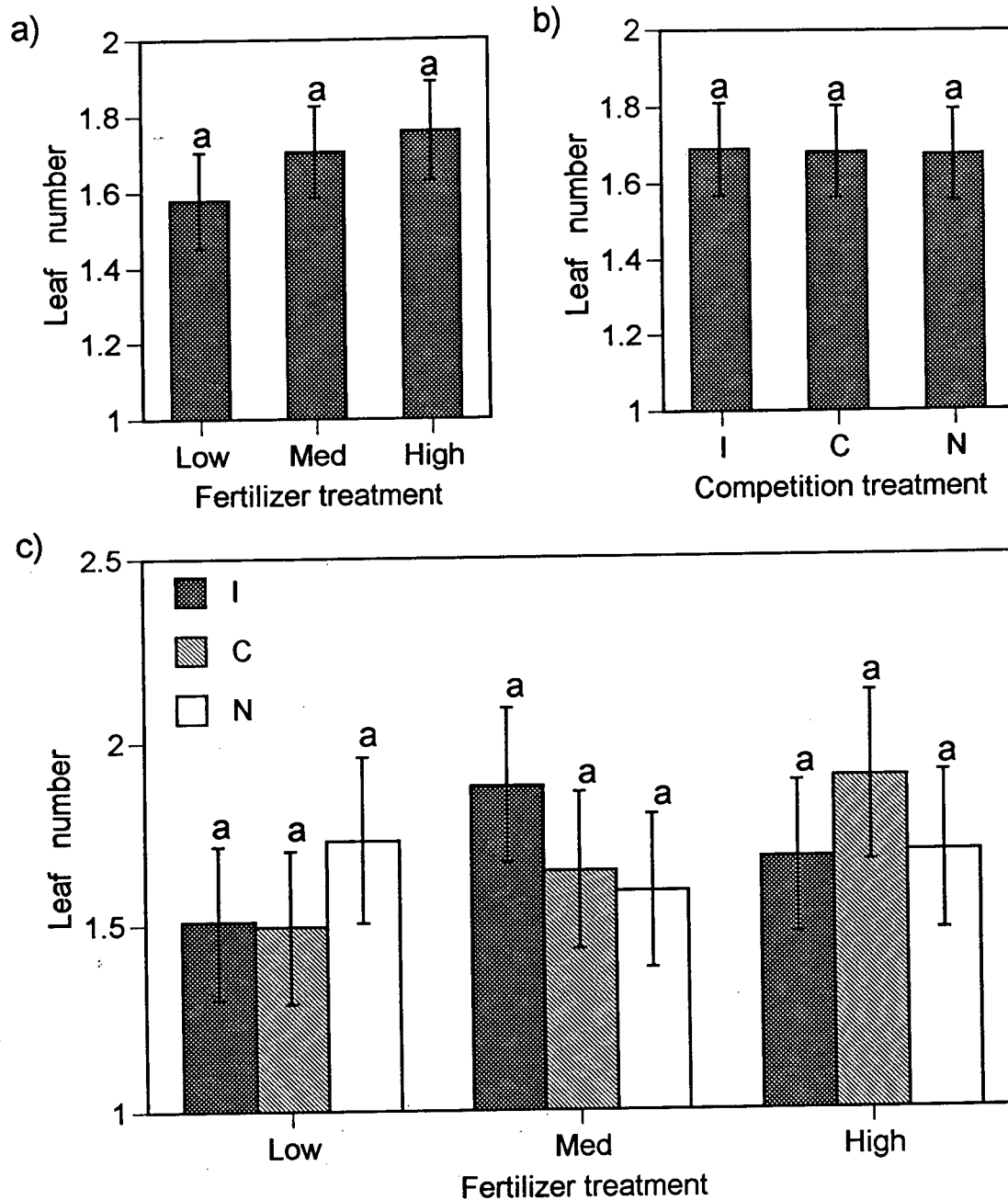
Fig. 17. Mean number of leaves (and S.E.) of *Mertensia paniculata* (with flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different (*P* > 0.05; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different (*P* > 0.05; LSD).
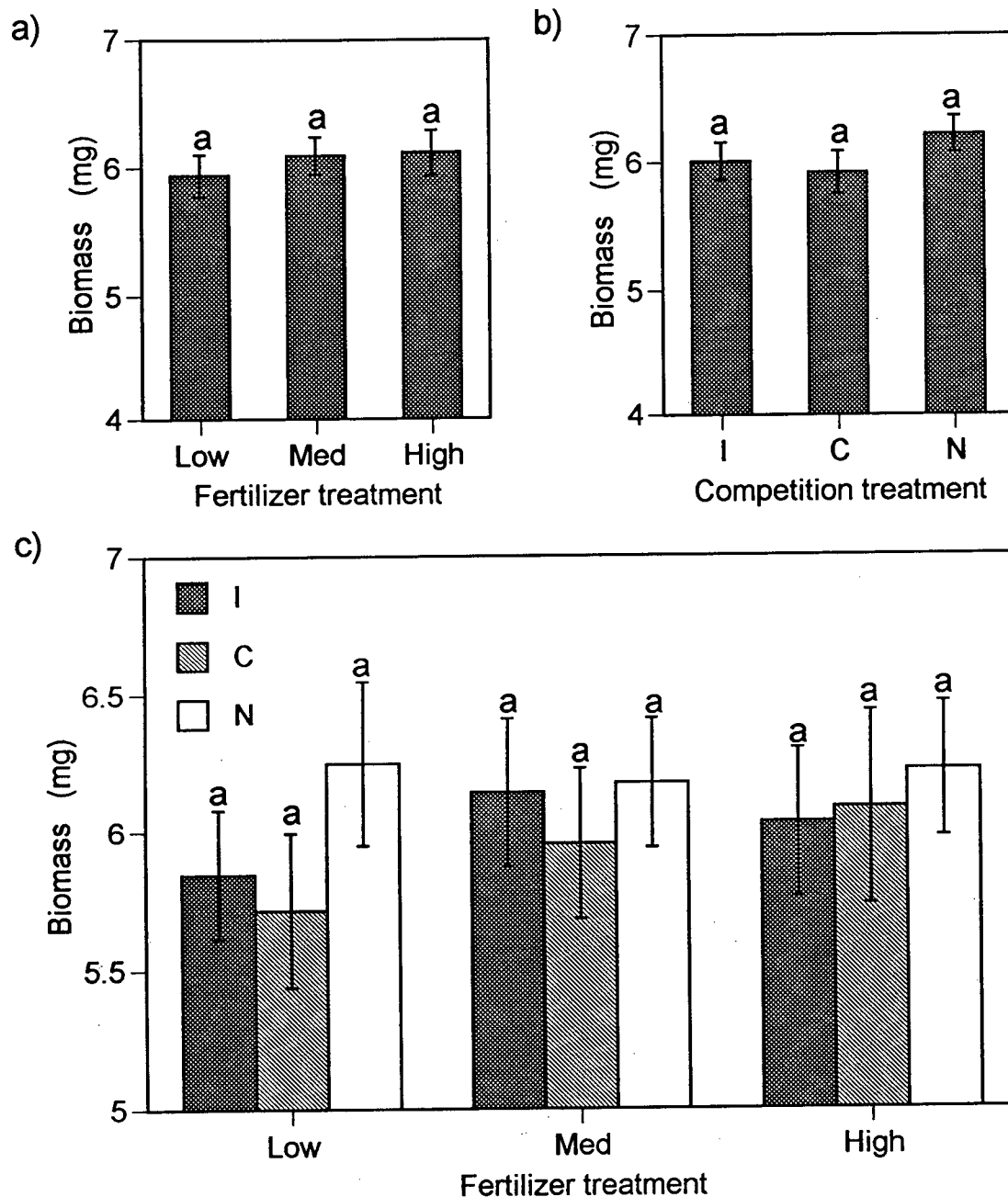
Fig. 18. Mean biomass (and S.E.) of *Mertensia paniculata* (without flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different ($P > 0.05$; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different ($P > 0.05$; LSD).

Fig. 19. Mean number of leaves (and S.E.) of *Mertensia paniculata* (without flowering individuals) by treatments. a) Comparison by fertilizer treatments; low, med, high. b) Comparison by competition treatments; I, C, N. c) Comparison by competition treatments at each fertility level. For a) and b), columns sharing the same letter are not significantly different (*P* > 0.05; LSD). For c), columns within each fertility level with the same letter represent competition treatment which are not significantly different (*P* > 0.05; LSD).

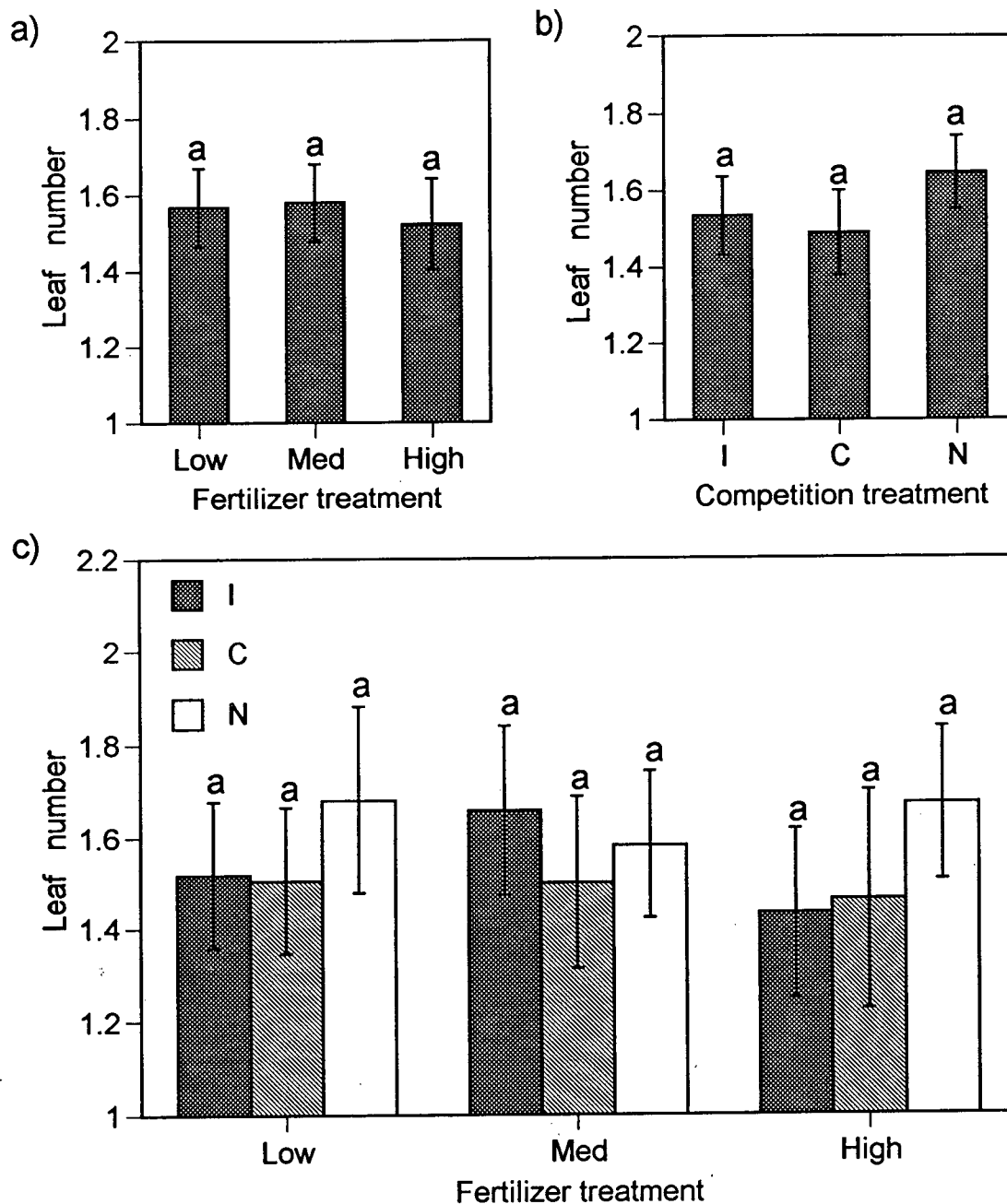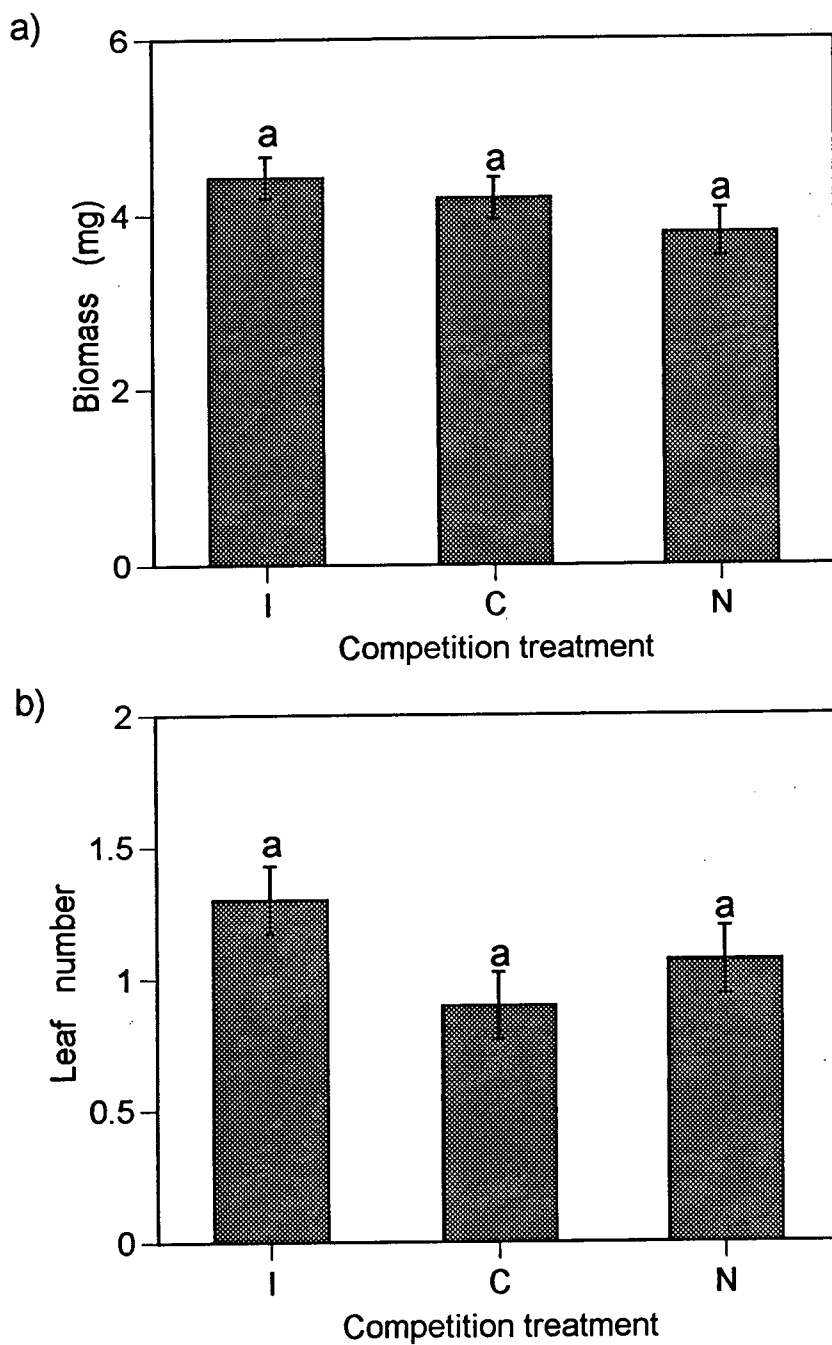**Fig. 20.** Mean (and S.E.) a) biomass and b) number of leaves of *Anemone parviflora* by competition treatment (I, C, and N) at low fertility. Columns sharing the same letter are not significantly different (*P* > 0.05; LSD).

C. Results from calculating indices

1. Notes in calculations

For *A. millefolium* and *M. paniculata*, competition intensity was calculated only when the flowering individuals were included. This was done because excluding flowering individuals had little effect on the results. Also, including the flowering individuals would increase the sample size which is likely to give more precise adjusted means. Neither competition intensity nor reduction relative to maximum growth were calculated for *A. parviflora* since most of the target individuals died with the addition of fertilizer.

2. Competition intensity by fertility level

Achillea millefolium

Total competition intensity (TC) of biomass at low fertility was not statistically significant from zero (Fig. 21), but considerably larger when compared to other species at low fertility. TC increased and became statistically significant at medium fertility, but was insignificant at the high fertility level. Root competition intensity (RC) also was significant only at the medium fertility level. In contrast, shoot competition intensity (SC) appeared greatest only at the high fertility level, although it was not significant.

When leaf number is used in the calculation of the index, TC shows results parallel to those results using biomass (Fig. 22). With increasing fertility, RC declines while SC increases. However, significant difference from zero is only found at medium fertility of RC.

Festuca altaica

Significant differences were not found in any of the calculations done for *F. altaica.* However, TC and SC of leaf number increased with increasing fertility while RC remained constant (Fig. 22). TC, RC, and SC of biomass all showed the highest value at medium fertility (Fig. 21).

Lupinus arcticus

None of the indices showed any statistical difference from zero at any fertility level for both biomass and leaf number (Fig. 21, 22). For leaf number, there were increases in TC and SC while RC did not differ much from zero (Fig. 22). Results of biomass suggests no such trend (Fig. 21).

Mertensia paniculata

Results for *M. paniculata* did not show any statistical differences from zero in TC, RC, and SC at any fertility level for both biomass and leaf number (Fig. 21, 22). From the results using biomass (Fig. 21), RC had positive values at all fertility levels while all SC values were negative. No such trend may be found when using leaf number (Fig. 22), but, an increase in values may be found for SC.
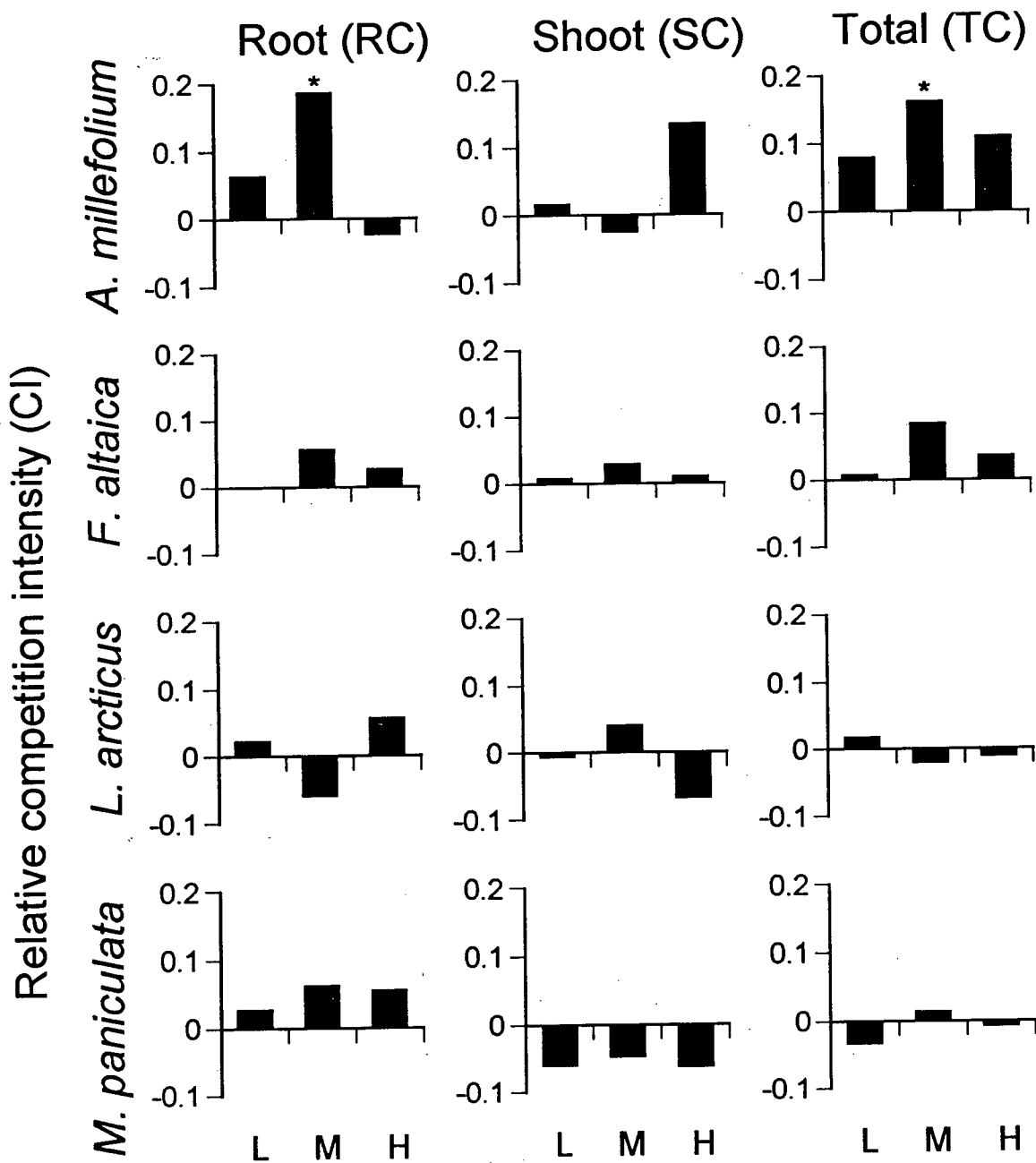
Fig. 21. Competition intensity indices (CI) calculated using biomass at different fertility levels by species. Each row of graphs indicates a different species, and root, shoot, and total competition intensity for that species. For calculations see Chapter 2. Within each graph, the x-axis represents fertility levels; L-low, M-medium, H-high. * indicates significantly different from zero ($P < 0.05$).
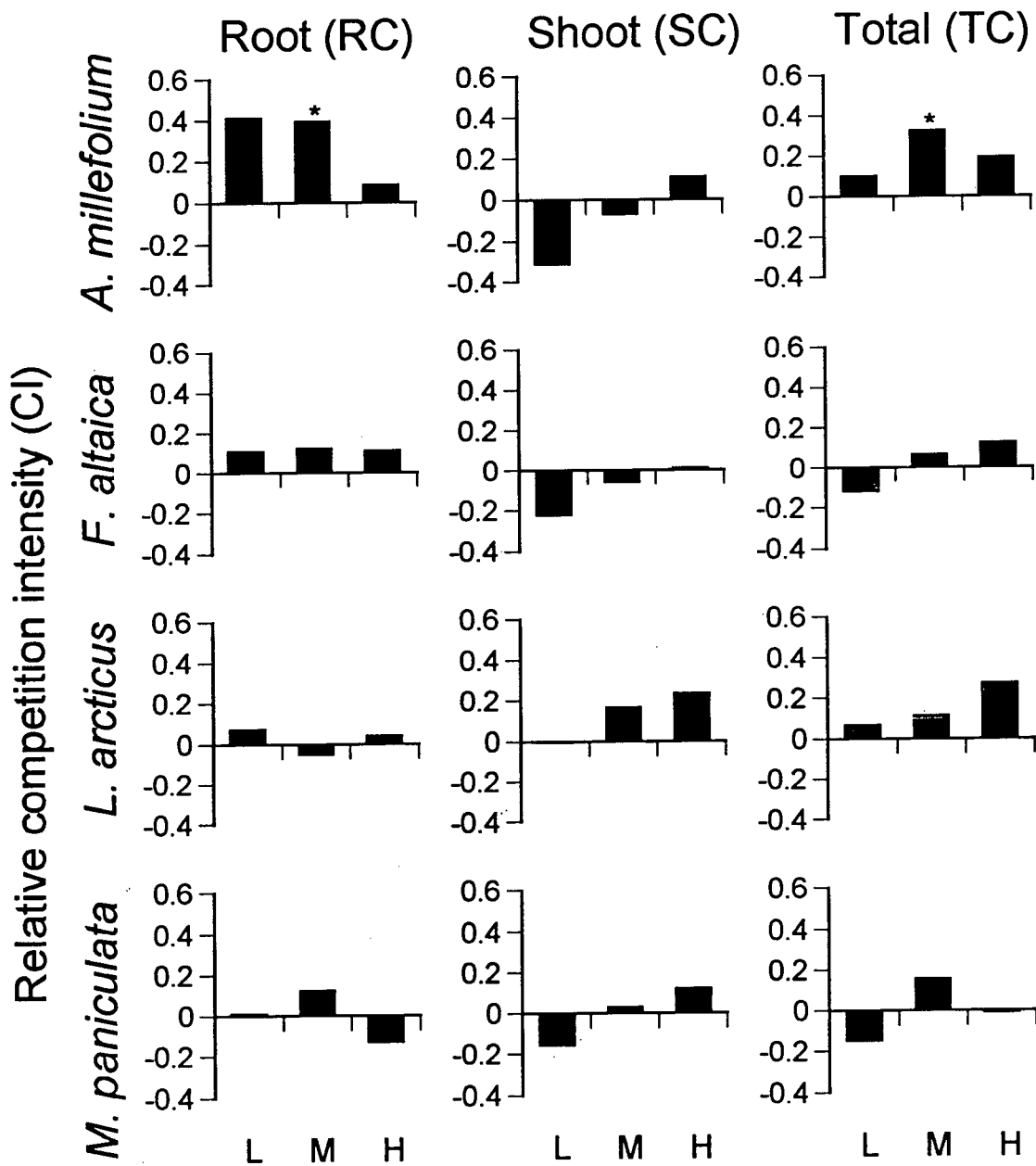
Fig. 22. Competition intensity indices (CI) calculated using number of leaves at different fertility levels by species. Each row of graphs indicates a different species, and root, shoot, and total competition intensity for that species. For calculations see Chapter 2. Within each graph, the x-axis represents fertility levels; L-low, M-medium, H-high. * indicates significantly different from zero ($P < 0.05$).

3. Calculation of reduction relative to maximum growth

Total reduction (RT) of *A. millefolium* and *F. altaica* in the natural habitat (= low fertility) is caused mostly by fertility (Fig. 23). For *L. arcticus* and *M. paniculata*, neither fertility nor competition seem to be limiting in the natural habitat (Fig. 23).

D. Surrounding vegetation

1. Leaf area index (LAI)

Regression analysis between LAI and biomass of surrounding vegetation showed a significant ($P < 0.001$) relationship (Fig. 24). This suggests that LAI is a good indicator of biomass surrounding the target individual.

The LAI of the surrounding vegetation within plots differed depending on the target species and on fertilizer treatments (Table 5). When the mean LAI in plots were grouped by target species, there were no significant differences between plots with *M. paniculata* and *A. millefolium* as target species, and between plots with *F. altaica* and *A. parviflora* as target species, but the two groups differed significantly (Fig. 25). However, the difference between the largest (*M. paniculata*) and the smallest (*A. parviflora*) mean value differed by only 4.25 per plot, which equates to 3.6 g per plot (= 14.4 g/m2) using the regression equation (Fig. 24). Thus, although it is statistically significant, this difference will probably not have a significant effect on the target individuals.
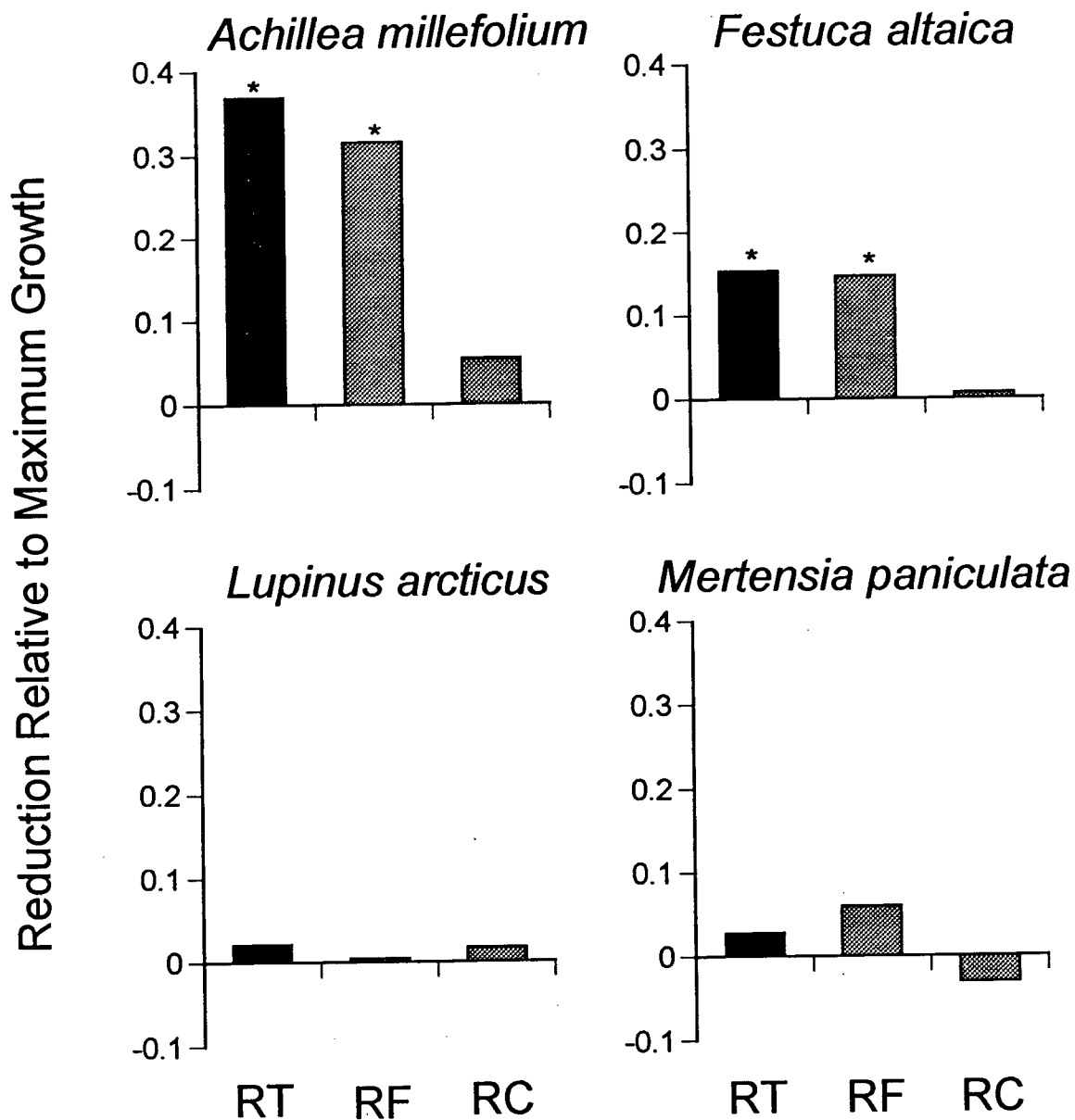
Fig. 23. Reduction relative to maximum growth by species. RT: Total reduction due to both nutrient limitation and competition; RF: Reduction caused by nutrient limitation; RC: Reduction caused by competition. * indicates significant difference from zero ($P < 0.05$).
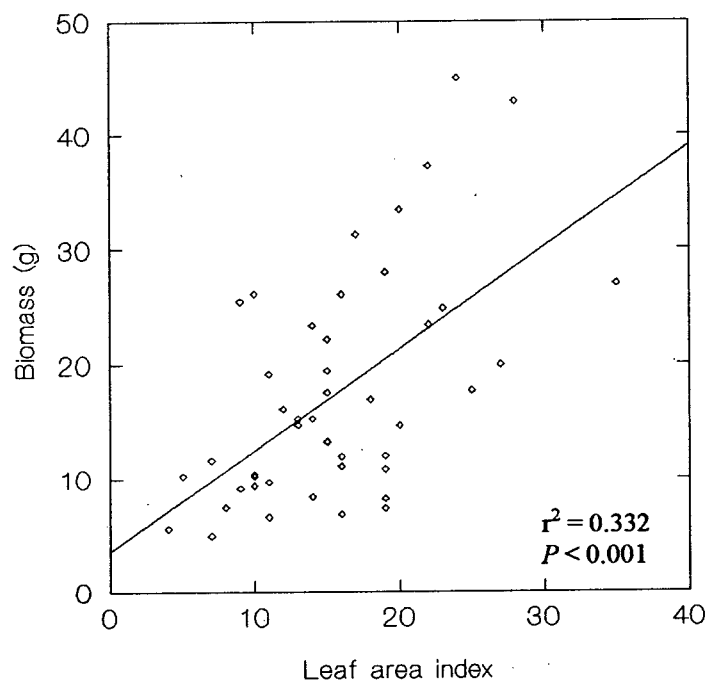
Figure 24. Regression between leaf area index of surrounding vegetation and its biomass. The relationship is described by the linear equation: Biomass = 3.621 + 0.886 (leaf area index) (N = 46).

Table 5. Results from analysis of variance (ANOVA) on factors influencing the leaf area index (LAI) of surrounding vegetation. No significant interactions were found in the analysis. Bold indicates $P < 0.05$.

Source	df	MS	F-ratio	P
Species	4	86.508	3.088	**0.020**
Fertilizer	2	165.900	5.922	**0.004**
Competition	1	0.008	0.000	0.986
Species * Fertilizer	8	27.671	0.988	0.451
Species * Competition	4	54.967	1.962	0.107
Fertilizer * Competition	2	1.233	0.044	0.957
Species * Fertilizer * Competition	8	36.317	1.296	0.256
Error	90	28.014		
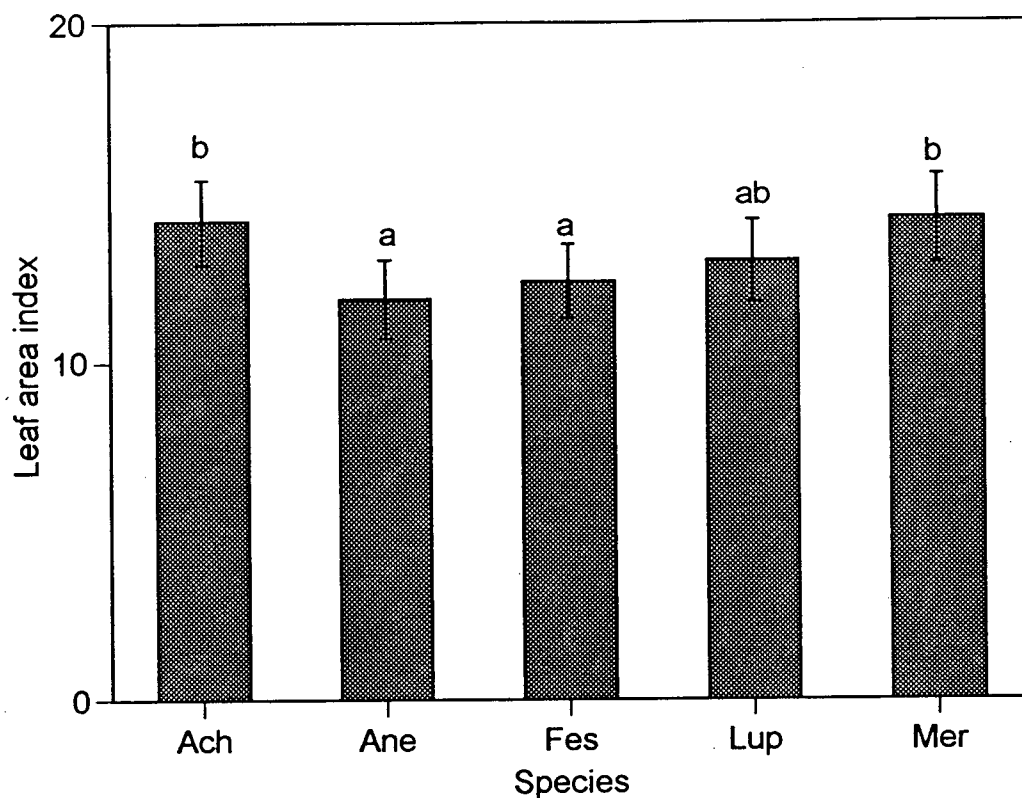
Figure 25. Mean values of leaf area index (and S.E.) within the plots grouped by target species (Ach = *Achillea millefolium*, Ane = *Anemone parviflora*, Fes = *Festuca altaica*, Lup = *Lupinus arcticus*, Mer = *Mertensia paniculata*). Columns sharing the same letter are not significantly different ($P > 0.05$; LSD).

When mean LAI values within plots were grouped by fertility treatments, the highest value was found at medium fertility (Fig. 26). This trend is also seen when they are grouped by fertility treatments for each target species separately (Fig. 27).

2. Species composition

The result of principal component analysis (PCA) on surrounding vegetation is given in Table 6. The general conclusion is that species composition within the plots do not differ critically depending on the target species. The species which occurred in almost all the plots were *F. altaica, L. arcticus*, and *Linnea borealis. Achillea millefolium* and moss were found quite frequently in the plots with *A. millefolium, A. parviflora*, and *Festuca altaica* as target individuals.
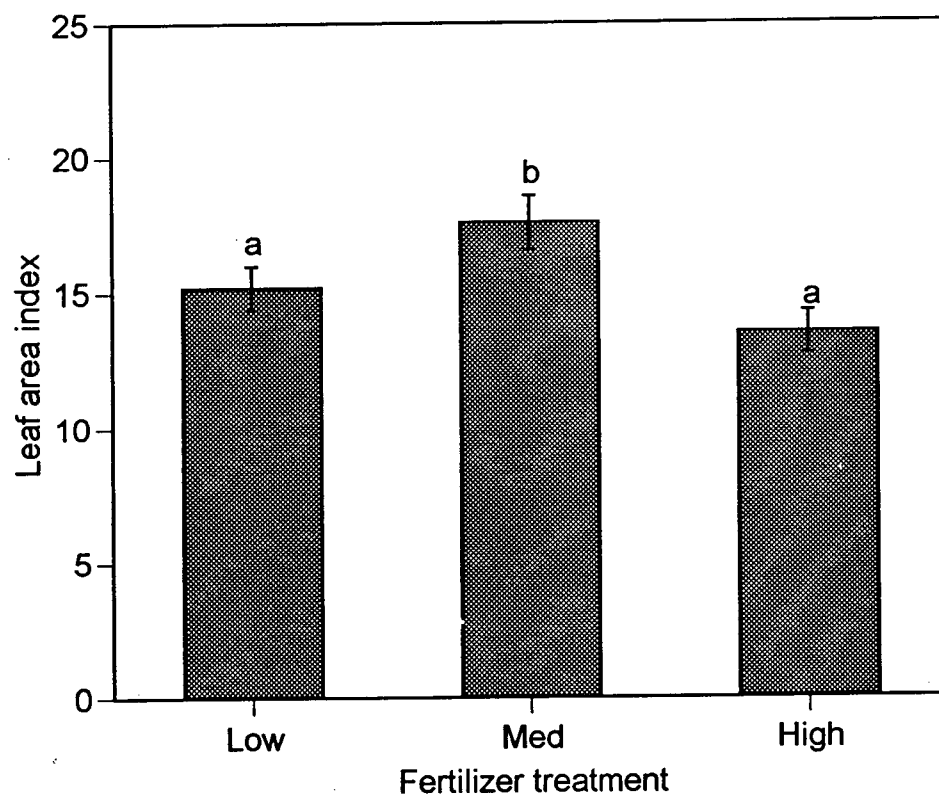
Figure 26. Mean values of leaf area index (and S.E.) within the plots grouped by fertility treatments; low, medium, and high. Columns sharing the same letter are not significantly different($P > 0.05$; LSD).
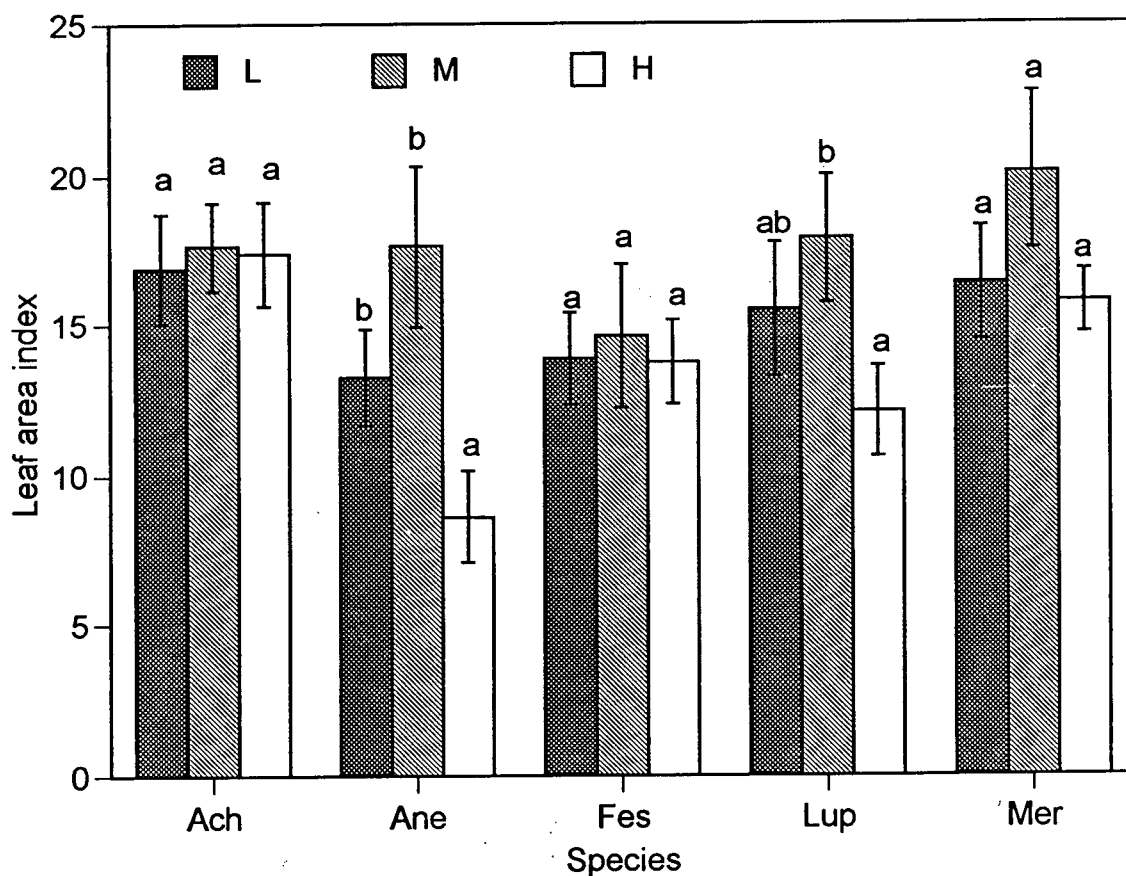
Figure 27. Mean values of leaf area index (and S.E.) within the plots grouped by fertilizer treatments (L - low, M - medium, H - high) for each target species (Ach = *Achillea millefolium*, Ane = *Anemone parviflora*, Fes = *Festuca altaica*, Lup = *Lupinus arcticus*, Mer = *Mertensia paniculata*). Columns sharing the same letter are not significantly different ($P > 0.05$; LSD).

Table 6. Results of PCA on surrounding vegetation within plots. Figures showing component loadings of each variable and scatterplots of plots grouped by target species are in Appendix 3.

Variables	Eigenvector (percent variance explained)			
	Factor 1 (14.5%)	Factor 2 (10.7%)	Factor 3 (10.1%)	Factor 4 (9.4%)
Achillea millefolium	-0.292	0.284	0.286	0.163
Anemone multifida	-0.203	-0.089	0.159	-0.432
Anemone parviflora	0.031	0.183	**-0.548**	0.172
Arctostaphylos rubra	0.099	-0.343	-0.483	0.404
Arctostaphylos uva-ursi	0.040	**-0.587**	0.062	-0.256
Festuca altaica	**-0.740**	0.084	-0.034	0.098
Linnea borealis	**0.606**	0.132	0.245	0.248
Lupinus arcticus	**0.582**	0.017	**0.514**	-0.034
Mertensia paniculata	-0.280	0.184	0.486	0.451
Senecio lugens	-0.012	**0.604**	-0.134	0.210
Solidago multiradiata	**-0.636**	-0.131	0.205	-0.092
Moss	0.043	0.495	-0.090	**-0.571**
Cladonia	0.125	0.347	-0.206	-0.309

Chapter 4. Discussion

The effect of fertility treatments

Models of Grime and Tilman predict increased plant growth with addition of fertilizer. However, based on his arguments of 'stress-tolerant' species, Grime also predicts that there should be little increase due to fertilizer application. Chapin (1991) supports this prediction by pointing out that plants adapted to low-resource environments grow very slowly, even when they are provided with additional supply of nutrients.

From the results of this research, the five species examined may be categorized into three groups based on their responses to fertilizer. The first, *A. millefolium* and *F. altaica*, responded positively to the addition of fertilizer by increasing both biomass and leaf number. This was the expected result of fertilizer application at the outset of this study. The second, *L. arcticus* and *M. paniculata*, did not respond, or responded very little to fertilizer application. This group appears to be consistent with Grime's prediction of 'stress-tolerators'. The last, *A. parviflora*, responded negatively to fertilizer addition and suffered increased mortality. Plants have an optimal level of nutrient concentration where further supplements of fertilizer do not promote growth. Continued increase beyond this level lead to toxicities and reduced growth (Salisbury and Ross 1992). Increases in biomass and leaf number were observed for *A. millefolium* (without flowering individuals) and *F. altaica* with increasing fertility; however, very little increase was observed from medium to high fertility levels. These results may indicate that growth is reaching an optimum. The decline in growth

of *A. parviflora* at high fertility levels may be a toxicity effect, but physiological studies were not done to confirm this.

In a fertilization experiment in the boreal forest trees, Chapin et al. (1983) showed that while early successional species such as *Populus tremuloides* (aspen), *P.* balsamifera (balsam poplar), and *Betula papyrifera* (white birch) responded positively to the addition of phosphate fertilizer, late successional species such as black spruce (*Picea mariana*) and white spruce (*Picea glauca*) did not. The response of *A. millefolium* and *F. altaica* seems to match the response of early successional trees, whereas *A. parviflora*, *L. arcticus*, and *M. paniculata* are consistent with that of late successional boreal forest trees. Bazzaz (1979) argued that early and late successional plants have many contrasting physiological attributes, such as rates of photosynthesis and resource acquisition, with the early successional species having higher values for both attributes. Accordingly, *A. millefolium* and *F. altaica* may be considered as early successional understory species, while *A. parviflora*, *L. arcticus*, and *M. paniculata* are late successional. This is further supported by the fact that *A. millefolium* and *F. altaica* are found more frequently in open sites compared to the other three species which are rarely found in the open. Conversely, *A. millefolium* and *F. altaica* become less frequent in closed forest canopy sites, while the other three species are quite abundant. The fact that this experiment was carried out in a small open patch within the boreal forest understory may have made it possible for all five species to coexist. As the canopy becomes more dense with time, it may be possible to see a shift in species composition from the early successional (*A. millefolium* and *F. altaica*) understory species to the later successional species (*A. parviflora*, *L. arcticus*, and *M. paniculata*).

Close by where these studies were done, is another, longer term, fertilization experiment (John and Turkington 1995). In that experiment, fertilizer has been applied to 16 plots, each 5 m x 5 m, since 1990, and changes in percent cover of the vegetation monitored. The results showed an increase in percent cover for *F. altaica* and *M. paniculata*, almost no changes for *A. millefolium*, and a slight decrease for *A. parviflora* and *L. arcticus*. The results by John and Turkington (1995) supported the results in this research for *A. parviflora*, *F. altaica*, and *L. arcticus*, but results for *A. millefolium* and *M. paniculata* were contrary; this research showed an increase in *A. millefolium*, and a decrease in *M. paniculata*.

Potential reasons for the differences may be related to the different strategies that species have for utilizing excess nutrients, as well as the different variables measured in the two studies. If a plant invests absorbed nutrients to expand the clones, by producing additional ramets, through vegetative reproduction rather than investing in its individual growth, it is possible to find an increase on measurements made at a population level (e.g. percent cover), while no increase may be detected at an individual level (e.g. biomass, leaf number). In contrast, if a plant invests absorbed nutrients on individual growth rather than producing new ramets, it is possible to find an increase in biomass, but not in percent cover. Thus, *M. paniculata* may be producing new ramets (former explanation), while *A. millefolium* invests in individual growth (latter explanation). The fact that *M. paniculata* is often found in clumps in the natural vegetation, while *A. millefolium* is not, may partially support this explanation. From this argument, it may not be correct to say that *M. paniculata* did not respond to the addition to fertilizer, but responded in a way that could

not have been detected by the measurements made. Another study in the same general area showed increases in growth (biomass, number of tillers, etc.) for both *A. millefolium* and *F. altaica* with application of nitrogen fertilizer over a two-year period which is consistent with the results from this study (Nams et al. 1993).

John and Turkington (1995) also observed a slight decrease in percent cover for *A. parviflora*, but not the drastic decrease as reported here. This may be due to the different amounts of fertilizer applied in the two experiments. John and Turkington (1995) applied 17.5 g N m^{-2}, 5 g P m^{-2}, and 2.5 g K m^{-2} per season, which were much smaller amounts than those applied in this research: 48 g N m^{-2}, 64 g P m^{-2}, and 48 g K m^{-2} (= medium fertility), and 96 g N m^{-2}, 128 g P m^{-2}, and 96 g K m^{-2} (= high fertility). The larger amounts of fertilizer applied in this study may have caused the higher mortality reported for *A. parviflora*.

The effect of competition treatments

Models of Tilman and Grime make different predictions on the intensity of competition in 'harsh' and low-resource (= low nutrient availability) environments such as the boreal forest understory. Tilman's model predicts that competition will be intense even in a low nutrient environment, but competition would be mainly for belowground resources. Grime, in contrast, predicts that the intensity of competition in a 'stressful' habitat such as the boreal forest should be very low, or absent.

The results reported here are consistent with Grime's prediction. For all five species investigated, neither biomass nor leaf number differed significantly among the competition

treatments at low fertility (= natural condition). Competition intensity indices (CI) for all species at low fertility were not significantly different from zero. Also, reduction relative to maximum growth indicated that competition is not a major limiting factor for the species studied. Thus, competition appears to play a very limited role in restricting the growth of the five herbaceous species examined in the boreal forest understory.

Several other studies have shown that competition may be constrained by stressful environments. Houle (personal communication) reported that interspecific competition was not significant in the coastal dune community of subarctic Quebec. Kadmon (1995) reported that total competition intensity was nonsignificant towards the less productive parts of a manipulated resource gradient in a desert system in Israel. Reader (1990) also reported that low nutrient supply can constrain competition by limiting plant growth in an abandoned pasture in Ontario.

In contrast, other studies have found significant competition intensity in sites which have low nutrient availability and may be categorized as a stressful environment. Wilson (1993) detected significant belowground competition intensity in Australian alpine heath and grassland. Wilson and Tilman (1991, 1993) likewise showed significant belowground competition in prairie in Minnesota. Belcher et al. (1995) also reported significant belowground competition in an alvar community (vegetation growing on thin soil over limestone rock) in Ontario.

The results of Wilson (1993), Wilson and Tilman (1991, 1993), and Belcher et al. (1995) reject Grime's prediction, that competition is not important in stressful and low nutrient availability habitats. However, this argument may be dismissed by merely stating

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that the study sites were not stressful enough in these four studies. One of the problems when testing Grime's prediction is determining a 'stressful habitat'. When do we label an environment as stressful? Unless this is strictly defined, Grime's predictions may never be rejected.

However, if all the above study sites were to be categorized as 'stressful' habitats, the differences in results may be related to differences in the range of biomass present per square meter. In this study, biomass ranged between 50 - 200 g/m^2. In the studies of Reader (1990) and Kadmon (1995), where competition was not found at low resource sites, biomass ranged between 200 - 400 g/m^2. In contrast, Belcher (1995) reported biomass up to 600 g/m^2, and Wilson and Tilman (1991, 1993) had between 400 - 1000 g/m^2; Wilson (1993) did not report biomass values. Thus, studies that did not find competition to be a limiting factor were done in low biomass sites, whereas the studies that detected competition were conducted in higher biomass sites. This difference may be determining the occurrence of competition.

The intensity of competition along a gradient of nutrient application

Debate exists whether the intensity of competition increases or remains constant along a gradient of nutrient availability. Grime's model predicts that all competition intensity (CI) values will increase with increasing nutrient availability. In contrast, Tilman's model predicts that total competition intensity (TC) will remain constant due to tradeoffs between root and shoot competition. However, based on Grime's arguments about stress-tolerance, it is also predicted that all CI values should remain close to zero at all fertility levels.

In this study, none of the competition intensity indices (root, shoot, and total) for *F. altaica, L. arcticus,* and *M. paniculata* showed statistical significance from zero at any of the fertility levels. This implies that competition intensity remained constant along the gradient with the index values always close to zero. This is consistent with Grime's prediction of how 'stress-tolerators' should respond to these manipulations. Since 'stress-tolerators' are adapted to low nutrient environments, physiologically they are not capable of efficiently acquiring applied nutrients. Therefore excess nutrients did not change the intensity of competition which remains close to zero.

The only significant differences detected were the effects of TC and root competition intensity (RC) at medium fertility for *A. millefolium* (for indices using both biomass and leaf number). Indices using leaf number for *A. millefolium* showed decreasing RC with increasing fertility level and increasing shoot competition intensity (SC). This supports Tilman's prediction that there should be a tradeoff for above- and belowground competition with increasing fertility. This tradeoff may also be seen from medium to high fertility using biomass for *A. millefolium*. However, since the significant values were found only at medium fertility of RC, it is not reasonable to conclude that the response of *A. millefolium* is entirely consistent with Tilman's predictions, although trends to support it were shown.

Although none of the competition intensity indices was significantly different from zero, an interesting trend is shown in changing competition intensity using biomass of *M. paniculata*. At all fertility levels, RC had positive values, indicating competition, while SC was all negative, suggesting facilitation. This implies that shading by the surrounding

vegetation led to increased biomass of the target individuals. *Mertensia paniculata* may have the characteristics of shade plants that are particularly sensitive to strong light (Levitt 1972).

Changes in values of TC along the gradient for *A. millefolium* shows a 'humpback' shape in calculations using both biomass and leaf number. This trend also occurs for TC using biomass for *F. altaica*, although the index values were not significantly different from zero at any fertility level. Interestingly, the surrounding vegetation within the experimental plots also responded to the addition of fertilizer in a 'humpback' manner along the gradient. This trend was observed regardless of species used as the target individual. Thus, there is less vegetation surrounding the target individual at high fertility level, which may explain why TC decreases at high fertility compared to medium fertility for *A. millefolium* and *F. altaica*.

When target individuals of each species were grouped by competition treatments and summed across all fertility treatments, significant responses to competition treatments were detected for *A. millefolium* and *F. altaica*. This fact may be an indication that increasing competition intensity does occur with increasing fertility, but may not have been detected due to the small sample size at each fertility level. Thus, grouping the data by competition treatments, which effectively increased sample size, may have led to significant competition treatment effects.

Significant competition treatment effects were detected only in those species that responded positively to the application of fertilizer. This implies that species that are able to increase nutrient uptake and grow after fertilization are also the ones most limited by neighbors. Since competition intensity was close to zero for *A. millefolium* and *F. altaica* at

the low fertility level, they have the ability to tolerate low nutrient levels. However, when there is a pulse of nutrients, they retain nutrients and compete for the nutrients with its neighbors. Thus, according to Grime's classification, these two species may fall somewhere between 'stress-tolerators' and 'competitors'. In contrast, the other three species, *A. parviflora*, *M. paniculata*, and *L. arcticus*, are typical 'stress-tolerators', and do not respond to the addition of fertilizer or removal of neighbors.

The general conclusion is that competition does not increase with increasing fertility, and at all fertility levels the intensity of competition is close to zero. This is consistent with Grime's prediction of 'stress-tolerators'. However, the fact that significant competition effects were found for *A. millefolium* and *F. altaica* when they are grouped together regardless of the fertility treatments, may indicate that sample sizes may not have been large enough to detect significant difference from zero when the fertility levels were analyzed separately.

Problems with competition intensity indices

*A*n important methodological issue in testing a theory is the need for clear and unambiguous definition of variables and how they are to be measured (Grace 1991). One of the problems associated with calculating a competition intensity index relates to the choice of variables to use in the calculation. Studies attempting to clarify the debate between Grime and Tilman have used different variables to calculate competition intensity. Some studies have used biomass or a measure of plant growth (Wilson and Keddy 1986, Wilson and Tilman 1991, 1993, Belcher et al. 1995), while others have used population attributes such as recruitment,

survival and population growth (Gurevitch 1986, Reader and Best 1989, Reader 1990). Since both types of studies have provided support for both Grime's and Tilman's predictions, simply making a distinction between the kinds of measurements will not automatically clarify the debate. However, as shown in this study, biomass and leaf number, which are highly correlated, did not show exactly the same results, although the differences were small. This suggests that different plant traits respond differently to competition and may result in different interpretations.

Another problem central to this debate is the method used to calculate competition intensity (Grace 1991, 1993, 1995). Campbell and Grime (1992) and Turkington et al. (1993) have shown that the use of absolute and relative competition intensity can lead to different conclusions. Both studies have shown that when competition was calculated as an absolute value, the intensity of competition increased as fertility increased, a result consistent with Grime's prediction. However, when competition intensity was calculated as a relative value, the results were consistent with Tilman's prediction that competition intensity should remain relatively constant along a nutrient availability gradient. In this study, although relative values of competition intensity are presented, absolute competition intensity was also calculated and produced similar conclusions as the relative value. This result was contradictory with the results shown in Campbell and Grime (1992) and Turkington et al. (1993).

The difference between this study and the other studies may be accounted for by the relationship between absolute and relative competition intensity. Figures 28a, b show the contour graphs of constant absolute and relative competition intensity. When the differences between X-axis (I-treatment) and Y-axis (N-treatment) values are small, contour lines of absolute and relative competition intensity are almost parallel to each other (Fig. 28c). However, when differences between I- and N-treatments are large and increase, contour lines of absolute and relative competition intensity cross each other at an ever increasing angle. This has great implications on how absolute and relative competition intensities change.

For example, suppose that A and B (Fig. 28c) are biomass values at natural soil fertility levels at two different sites. When fertilized, the values of both I- and N-treatments will change, and most often, will alter the values of absolute competition intensity (ACI) and relative competition intensity (RCI). Figure 28 has been fabricated to demonstrate the effects of this changes on A and B. Point A represents a habitat with low values of both ACI and RCI. When fertilized, the values of ACI and RCI in habitat A move to the position of A`. However, the figure shows that this shift results in almost no change in values of either ACI or RCI. In contrast, B represents a habitat with high values of ACI and RCI, and when it is fertilized, the shift to B` shows almost no change in RCI, but a dramatic increase in ACI.
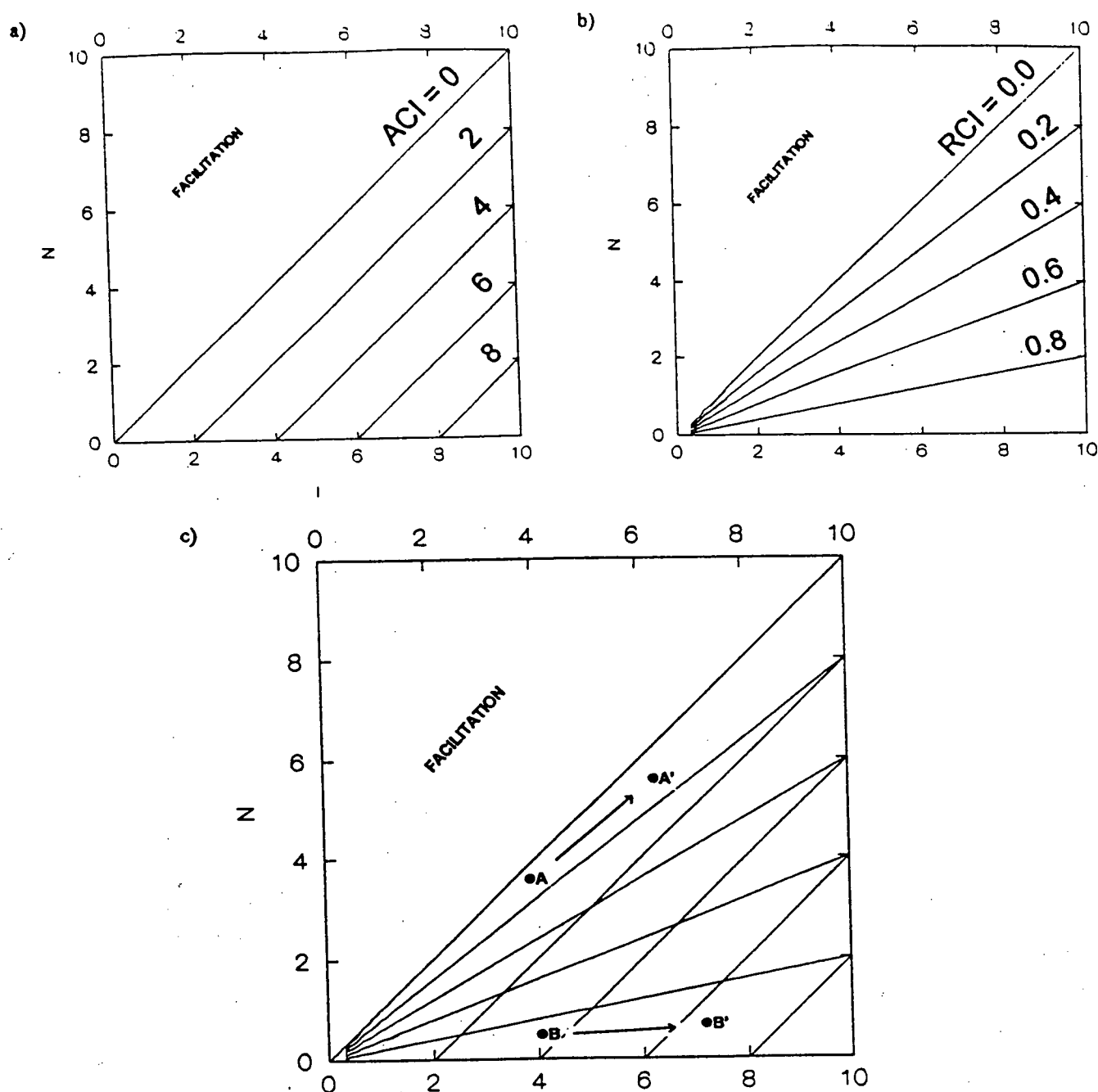
Figure 28. Illustration of the relationship between absolute and relative competition intensity. The x-axis is a measure of biomass when neighboring individuals are absent (the I-treatment). The y-axis is a measure of biomass when neighbors are present (the N-treatment). Values of absolute and relative competition intensity are indicated on the graph and calculated as : Absolute competition intensity (ACI) = I - N; Relative competition intensity (RCI) = (I - N) / I. The leading diagonal represents when there is no competition occurring (ACI=0, RCI=0); values below the leading diagonal show competition occurring; values above the leading diagonal indicate facilitation. a) Contour graphs showing constant absolute competition intensity values. b) Contour graphs showing constant relative competition intensity values.c) Contour graphs showing overlap of a) and b). Refer to text for explanation of points A, A`, B, and B`.

In short, the figure illustrates that in an environment where competition intensity stays very low (I- and N-treatment differences are small) along the gradient, both absolute and relative competition intensity tend to show similar patterns. In contrast, when competition intensity is high (I- and N-treatment differences large), absolute and relative competition intensity tend to show different trends. This may explain why the studies by Campbell and Grime (1992) and Turkington et al. (1993) showed differences in absolute and relative competition intensity, while in this study, where competition intensity remained low along the increasing fertility gradient, no differences between absolute and relative competition intensity indices were observed.

Response to treatments by species, and coexistence

As predicted in Chapter 1, coexisting species may have similar responses to treatments as they have converged to the same habitat condition. In contrast, one can also argue that coexisting species should have different responses to treatments so as to coexist.

The five species investigated in this research showed different responses to the addition of fertilizer and removal of neighbors. Achillea millefolium and *F.* altaica responded positively to increasing levels of fertilizer, and showed some limitation by the presence of neighbors. In contrast, *L.* arcticus and *M.* paniculata showed almost no response to treatments while A. parviflora showed negative response to fertilizer treatments. DiTommasso and Aarssen (1991), Wilson (1993), and Wilson and Tilman (1995) also reported different responses to altered environments by different species living in the same community.

The differences in competitive response among species may contribute to their coexistence (Bazzaz 1990; Wilson and Tilman 1995). Since only small differences in competitive response are required for coexistence in mathematical models (Tilman 1988), the divergence in competitive response noted in this study may also be an mechanism permitting coexistence of understory plants in the boreal forest. However, in the boreal forest understory, species may not necessarily have to show differences in their response in order to coexist. Despite the observed differences between *A. millefolium* and *F. altaica* and the other three species in their response to fertilizer treatments, no such "nutrient pulses" occur naturally in this system; thus, the differences in ability to acquire nutrients do not confer any advantage. Also, the apparent lack of competition with surrounding vegetation suggests that differences in competitive responses among the species may play only a minor role in the limiting distribution of a species or growth of an individual. In a severe environment such as the boreal forest understory, the primary strategy of the species is to stay alive, which is equivalent to Grime's 'stress-tolerators'. Thus, coexistence in a given area would depend largely on the species' ability to disperse into that area and their ability to remain once having established.

However, the differences in response may be important for their longer term survival and distribution when the environment change. For example, the frequency of the five species changes dramatically from closed to more open forest patches, where more sunlight reaching the ground surface produces warmer and fertile soil, and more vegetation cover. Such situations may be created by natural disturbances such as a fire. The species that

responded positively to the fertilizer application, *A. millefolium* and *F. altaica*, are seen much more frequently in open areas while the other three are, in most cases, absent.

In some competition studies (Reader 1990; Belcher et al. 1995), single indicator species (phytometers) are used to measure competition intensity within a community. However, as seen from the results presented here, species within the community may respond differently to the treatments. Therefore, the result of measuring competition intensity using a single indicator species will depend mainly on response characteristics of the particular indicator species used and may lead to erroneous interpretations if applied to broadly. Competition intensity of a community as a whole is a sum of responses of every species within that habitat rather than one representative species in that community.

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Appendix 1. Relationship between the covariate and its biomass

Here, the relationship between the measured covariate and its biomass is investigated. In early June, 1995, emerging buds of *Achillea* millefolium, *Lupinus arcticus*, and *Mertensia paniculata* were randomly spotted. They were all measured for the covariate in question which depends on the species, then immediately harvested, oven dried, and weighed. The weighed biomass were log-transformed and then regression analysis were done on each species separately.

a) *Achillea millefolium* (N = 30)

Independent variable (covariate)	- Longest leaf length (cm)	
Dependent variable	- Biomass (mg, log-transformed)	

Analysis of variance

Source	SS	DF	MS	F-ratio	P
Regression	11.934	1	11.934	66.169	0.000
Residual	5.050	28	0.180		

$r^2 = 0.703$
$P < 0.001$
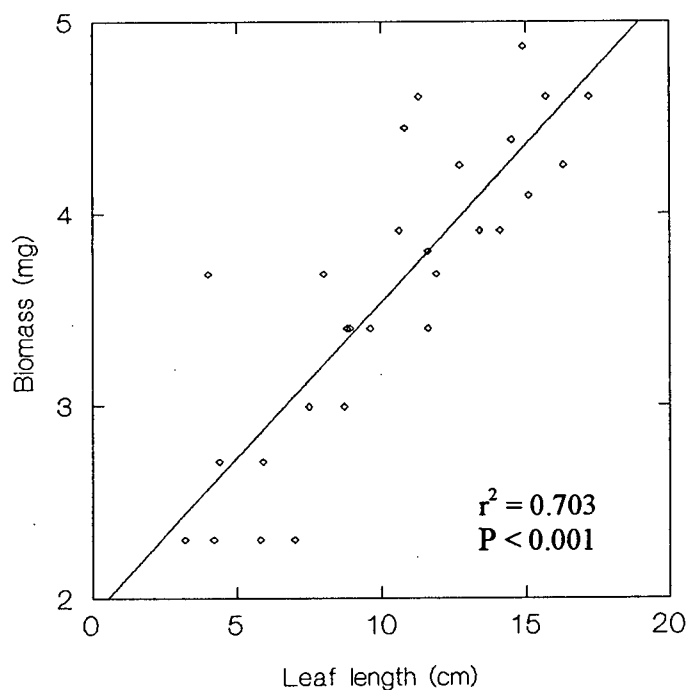
b) *Lupinus arcticus* (N = 30)

Independent variable (covariate)   - Clump diameter (cm)
Dependent variable   - Biomass (mg, log-transformed)

Analysis of varaiance

Source	SS	DF	MS	F-ratio	P
Regression	8.052	1	8.052	34.331	0.000
Residual	6.567	28	0.235		

$r^2 = 0.551$
$P < 0.001$

c) *Mertensia paniculata* (N = 27)

Independent variable (covariate)   - Longest leaf length (cm)
Dependent variable   - Biomass (mg, log-transformed)

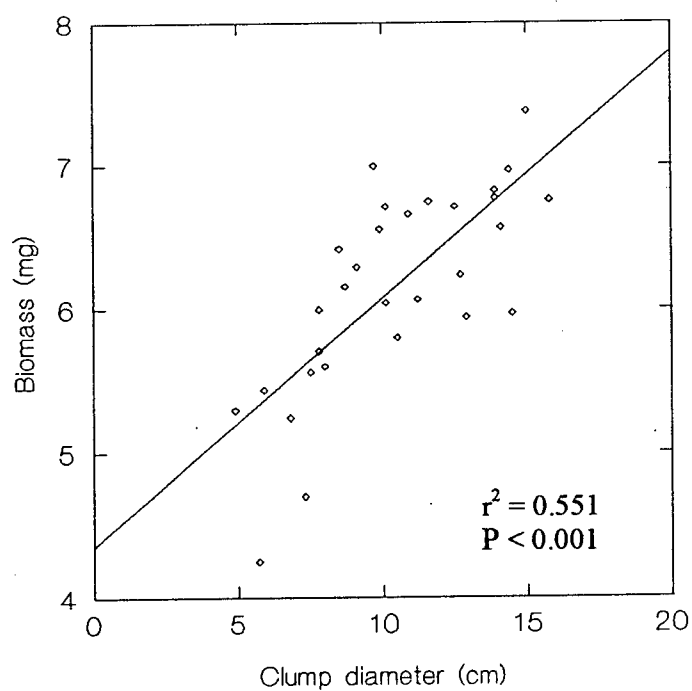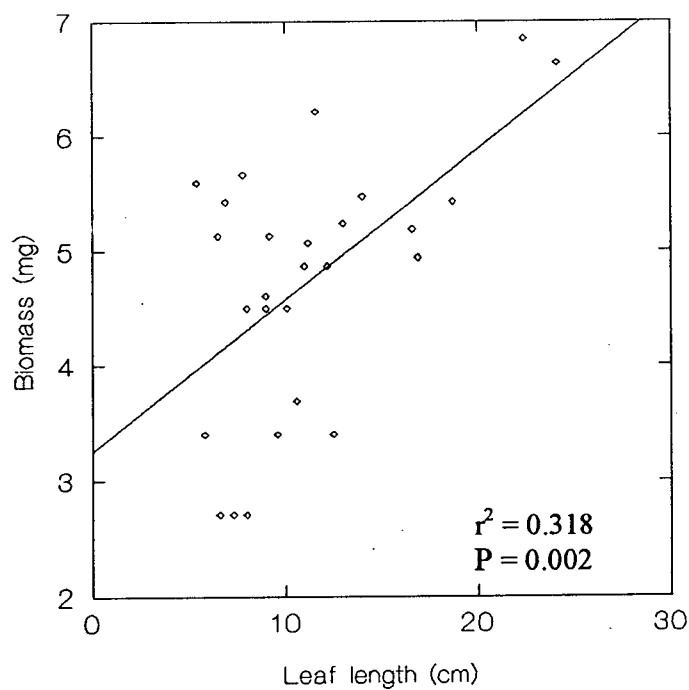Analysis of variance

Source	SS	DF	MS	F-ratio	P
Regression	10.600	1	10.600	11.654	0.002
Residual	22.739	25	0.910		

Scatter plot of Biomass (mg) versus Leaf length (cm) with regression line. $r^2 = 0.318$, $P = 0.002$

Appendix 2. ANCOVA / ANOVA Table

Abbreviations : FERT ... Fertility Treatment   COMP... Competition treatment
COV ... Covariate

1. *Achillea millefolium* (with flowering individuals included)

a) biomass (N=35)

Source	SS	DF	MS	F-ratio	P
FERT	24.179	2	12.090	30.261	0.000
COMP	2.746	2	1.373	3.437	0.048
FERT*COMP	2.036	4	0.509	1.274	0.307
COV	11.404	1	11.404	28.545	0.000
ERROR	9.988	25	0.400		

b) leaf number (N=34)

Source	SS	DF	MS	F-ratio	P
FERT	4.346	2	2.173	11.133	0.000
COMP	1.564	2	0.782	4.006	0.032
FERT*COMP	0.669	4	0.167	0.857	0.503
COV	4.740	1	4.740	24.289	0.000
ERROR	4.684	24	0.195		

2. *Achillea millefolium* (without flowering individuals)

a) biomass (N=29)

Source	SS	DF	MS	F-ratio	P
FERT	16.972	2	8.486	19.720	0.000
COMP	1.468	2	0.734	1.705	0.208
FERT*COMP	1.807	4	0.452	1.050	0.408
COV	6.119	1	6.119	14.220	0.001
ERROR	8.176	19	0.430		

b) leaf number (N=29)

Source	SS	DF	MS	F-ratio	P
FERT	1.811	2	0.906	6.268	0.008
COMP	1.019	2	0.510	3.527	0.050
FERT*COMP	0.434	4	0.109	0.751	0.570
COV	0.994	1	0.994	6.882	0.017
ERROR	2.754	19	0.144		

3. *Festuca altaica*

a) biomass (N=34)

Source	SS	DF	MS	F-ratio	P
FERT	5.410	2	2.705	13.789	0.000
COMP	0.504	2	0.252	1.284	0.295
FERT*COMP	0.320	4	0.080	0.407	0.802
COV	5.152	1	5.152	26.259	0.000
ERROR	4.708	24	0.196		

b) leaf number (N=34)

Source	SS	DF	MS	F-ratio	P
FERT	4.294	2	2.147	11.628	0.000
COMP	1.425	2	0.712	3.858	0.035
FERT*COMP	0.985	4	0.246	1.333	0.286
COV	4.867	1	4.867	26.359	0.000
ERROR	4.432	24	0.185		

4. *Lupinus arcticus*

a) biomass (N=34)

Source	SS	DF	MS	F-ratio	P
FERT	0.002	2	0.001	0.003	0.997
COMP	0.039	2	0.020	0.059	0.943
FERT*COMP	0.842	4	0.211	0.633	0.644
COV	11.873	1	11.873	35.726	0.000
ERROR	7.976	24	0.332		

b) leaf number (N=33)

Source	SS	DF	MS	F-ratio	P
FERT	1.902	2	0.951	2.736	0.086
COMP	0.961	2	0.480	1.382	0.271
FERT*COMP	0.508	4	0.127	0.365	0.831
COV	5.173	1	5.173	14.881	0.001
ERROR	7.995	23	0.348		

5. *Mertensia paniculata* (with flowering individuals)

a) biomass (N=35)

Source	SS	DF	MS	F-ratio	P
FERT	0.427	2	0.213	0.933	0.406
COMP	0.789	2	0.395	1.725	0.199
FERT*COMP	0.091	4	0.023	0.099	0.982
COV	10.236	1	10.236	44.765	0.000
ERROR	5.717	25	0.229		

b) leaf number (N=36)

Source	SS	DF	MS	F-ratio	P
FERT	0.174	2	0.087	0.496	0.614
COMP	0.002	2	0.001	0.005	0.995
FERT*COMP	0.447	4	0.112	0.639	0.640
COV	1.069	1	1.069	6.112	0.020
ERROR	4.549	26	0.175		

6. *Mertensia paniculata* (without flowering individuals)

a) biomass (N=29)

Source	SS	DF	MS	F-ratio	P
FERT	0.133	2	0.067	0.308	0.738
COMP	0.442	2	0.221	1.023	0.379
FERT*COMP	0.181	4	0.045	0.209	0.930
COV	10.668	1	10.668	49.346	0.000
ERROR	4.108	19	0.216		

b) leaf number (N=30)

Source	SS	DF	MS	F-ratio	P
FERT	0.014	2	0.007	0.069	0.933
COMP	0.123	2	0.062	0.607	0.555
FERT*COMP	0.092	4	0.023	0.226	0.921
COV	1.439	1	1.439	14.152	0.001
ERROR	2.034	20	0.102		

7. *Anemone parviflora* (ANOVA table)

a) biomass (N=11)

Source	SS	DF	MS	F-ratio	P
COMP	0.688	2	0.344	1.557	0.269
ERROR	1.768	8	0.221		

b) leaf number (N=12)

Source	SS	DF	MS	F-ratio	P
COMP	0.326	2	0.163	2.475	0.139
ERROR	0.592	9	0.066		

# Appendix 3. Results of PCA on surrounding vegetation within plots.

A.   Component loadings of each variable (Factor 1 and 2).
B.   Component loadings of each variable (Facror 3 and 4).
C.   Scatterplots of plots grouped by target species (Factor 1 and 2).
D.   Scatterplots of plots grouped by target species (Factor 3 and 4).
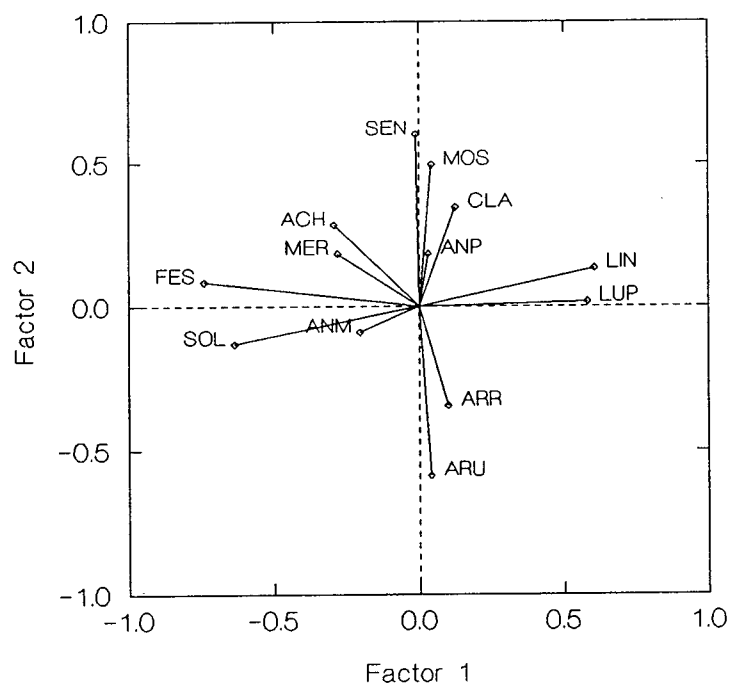
A. Component loadings of each variable for factors 1 and 2. ACH: *Achillea millefolium*. ANM: *Anemone multifida*. ANP: *Anemone parviflora*. ARR: *Arctostaphylos rubra*. ARU: *Arctostaphylos uva-ursi*. FES: *Festuca altaica*. LIN: *Linnea borealis*. LUP: *Lupinus arcticus*. MER: *Mertensia paniculata*. SEN: *Senecio lugens*. SOL: *Solidago multiradiata*. MOS: Moss. CLA: *Cladonia* spp.
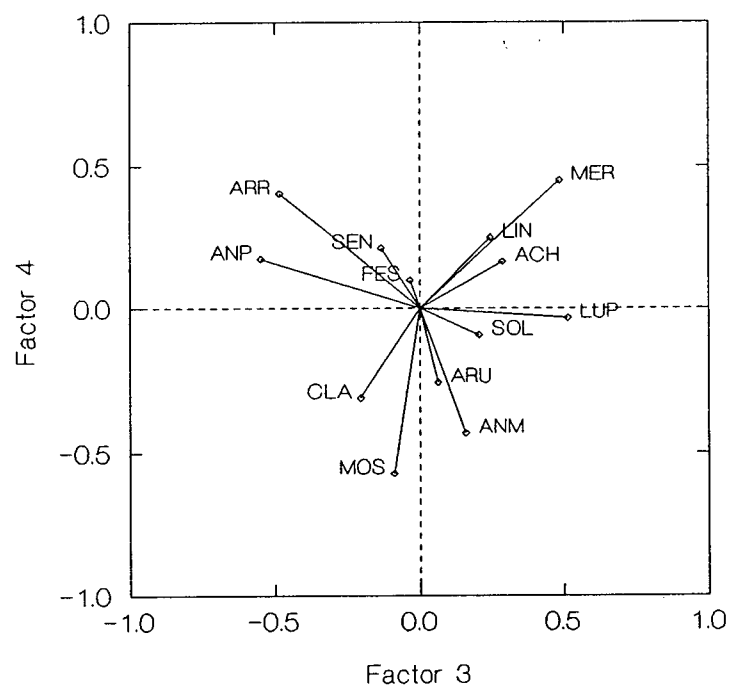
B. Component loadings of each variable for factor 3 and 4. ACH: *Achillea millefolium.* ANM: *Anemone multifida.* ANP: *Anemone parviflora.* ARR: *Arctostaphylos rubra.* ARU: *Arctostaphylos uva-ursi.* FES: *Festuca altaica.* LIN: *Linnea borealis.* LUP: *Lupinus arcticus.* MER: *Mertensia paniculata.* SEN: *Senecio lugens.* SOL: *Solidago multiradiata.* MOS: Moss. CLA: *Cladonia* spp.
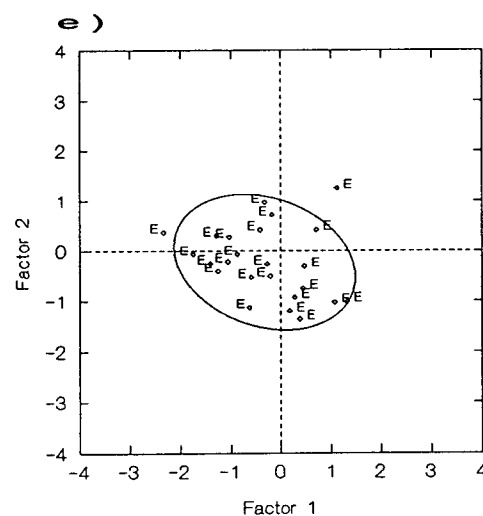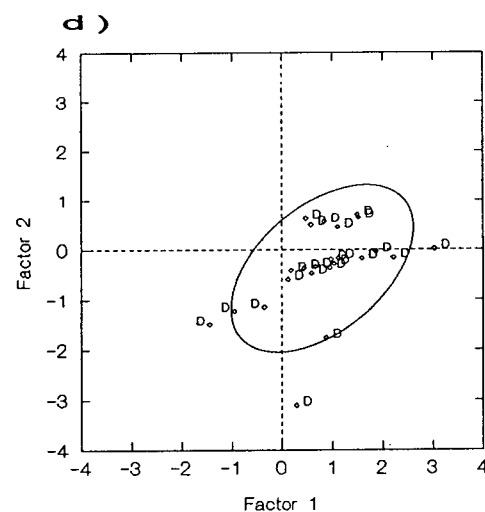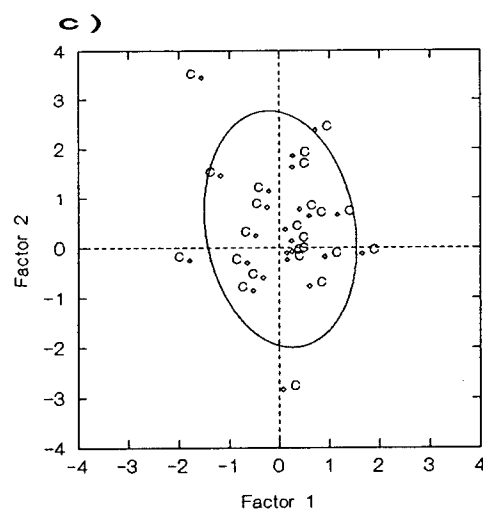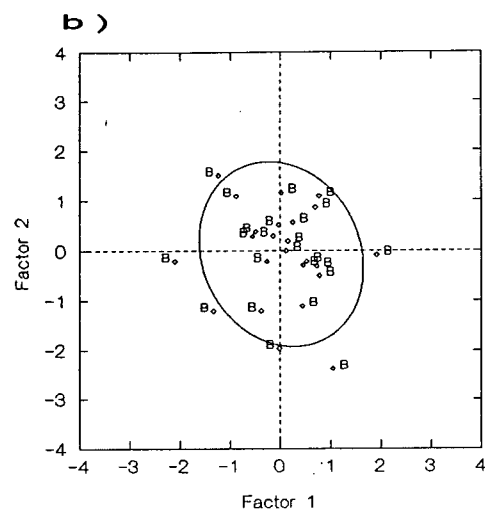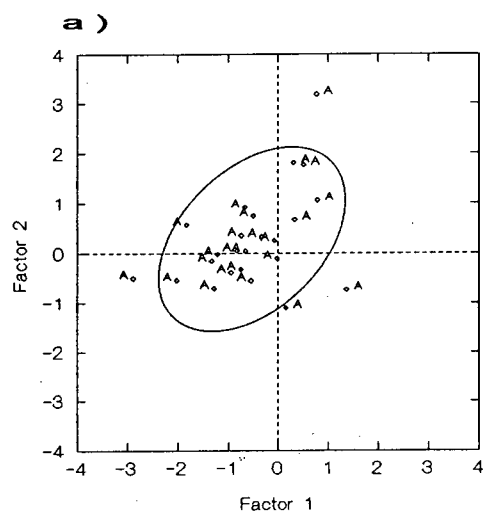
C. Scatterplots of plots grouped by target species (Factors1 and 2).
(80% ellipsoids).
   a) *Achillea millefolium*
   b) *Anemone parviflora*
   c) *Festuca altaica*
   d) *Lupinus arcticus*
   e) *Mertensia paniculata.*
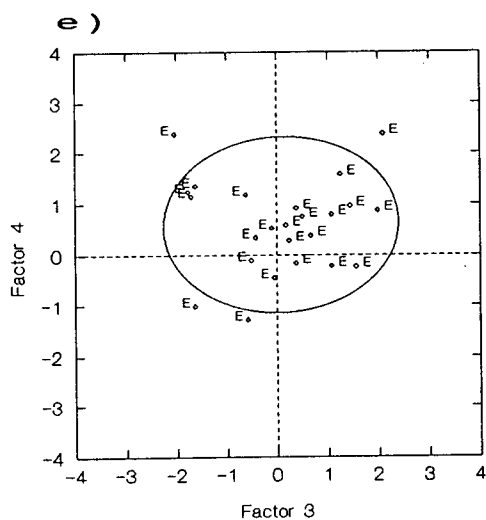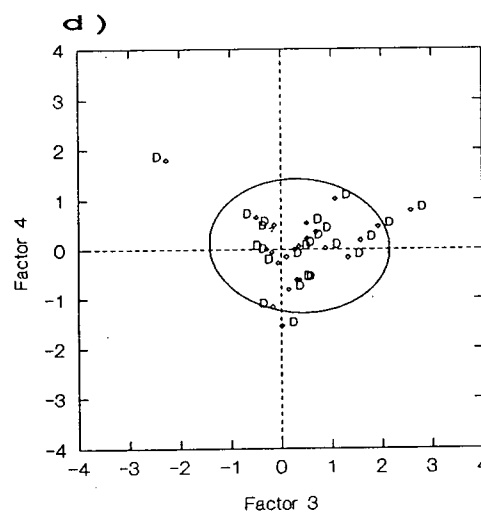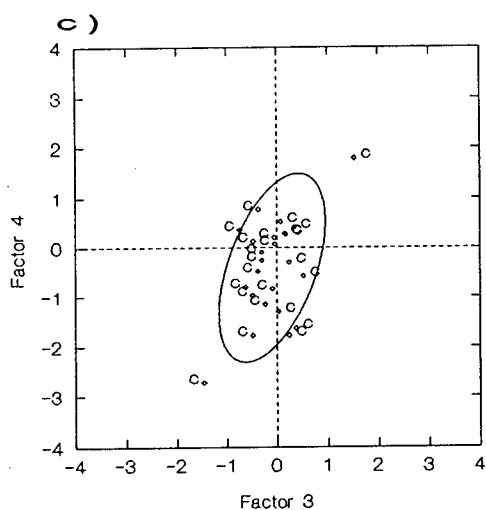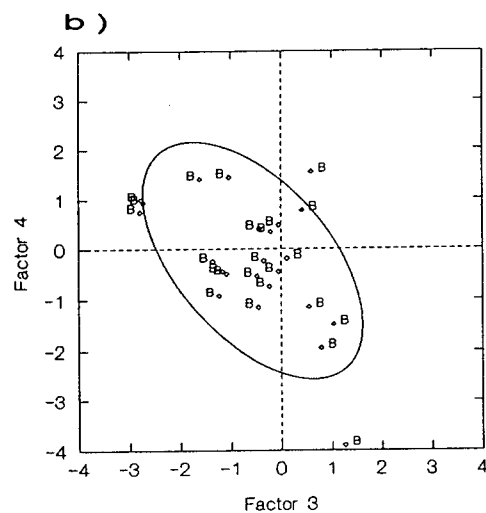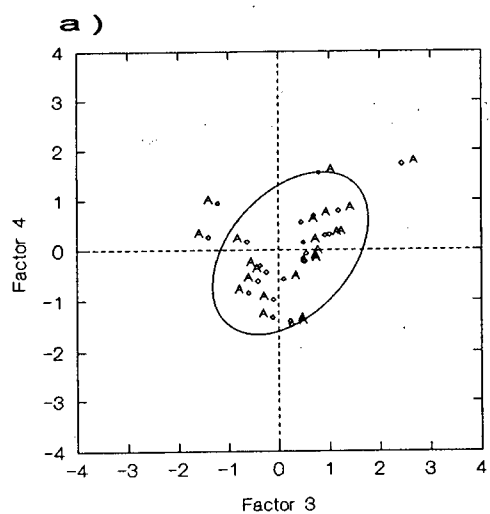
D. Scatterplots of plots grouped by target species (Factors 3 and 4). (80% ellipsoids).

a) *Achillea millefolium*
b) *Anemone parviflora*
c) *Festuca altaica*
d) *Lupinus arcticus*
e) *Mertensia paniculata.*