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Source: *Arctic, Antarctic, and Alpine Research*, Vol. 37, No. 4 (Nov., 2005), pp. 602-610
Published by: INSTAAR, University of Colorado
Stable URL: http://www.jstor.org/stable/4095880
Accessed: 17-06-2016 11:31 UTC

Arctic, Antarctic, and Alpine Research, Vol. 37, No. 4, 2005, pp. 602–610

Experimental Investigation of Fertilization and Irrigation Effects on an Alpine Heath, Northwestern Caucasus, Russia

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Abstract

We investigated the response of an alpine lichen heath plant community to an increase in soil nutrient and water availability. A 5-yr experiment—including additions of calcium, phosphorus, nitrogen, and nitrogen + phosphorus as well as irrigation—was conducted in northwestern Caucasus, Russia, at 2800 m above sea level. Number of plants and generative shoots per species were counted annually. The plant-community composition started to change during the second year of treatments. Plant density and flowering of the community is co-limited by nitrogen and phosphorus. Irrigation and calcium additions caused minimal changes. The total number of forb plants per square meter was not influenced by treatments, whereas the total number of graminoid plants slightly increased in response to P treatment and strongly increased in response to N + P treatment. Forbs responded to N and N + P treatments by an increase in the number of generative shoots. Individual species differed in their response to treatments. Only clonal species responded to experimental treatments, except for one annual nonclonal species, which increased its abundance in response to irrigation. Biodiversity estimated by the Shannon-Wiener index decreased under N + P treatment. Species number was not affected by any of the treatments.

Introduction

The influence of soil-resource availability on the structure of plant communities was studied extensively in the in the 1980s and 1990s (Tilman, 1982; Bowman et al., 1993; Shaver and Chapin, 1995). It is commonly agreed that nitrogen, phosphorus, and water are the most important soil resources for plant growth (Marschner, 2002). Körner (2003) claimed that, owing to the low mineralization rate, nitrogen is the most important nutrient for productivity of alpine plant species. The influence of other nutrients (phosphorus, in particular) and interactions between nutrients are less investigated. Previous research has indicated that soil moisture is also a very important factor limiting the production of alpine plant communities (Billings, 1974; Walker et al., 1994). Fisk et al. (1998) showed that the highest production of an alpine plant community is reached at medium soil moisture. Nevertheless, there are few experimental investigations (e.g., Bowman et al., 1995) of consequences of water-availability manipulations in alpine tundra.

Many fertilization experiments have indicated that species differ in their response to release from nutrient and water limitation (e.g., Chapin and Shaver, 1985; Press et al., 1998a). Thus, if the total plant-community biomass increases in response to nutrient additions, this is a result of a disproportionate increase of several species and a decrease of others (Grime, 1973; Bowman and Fisk, 2001). Besides biomass increase, nutrient additions may provoke a greater reproductive effort (Henry et al., 1986), resulting in increased flowering. However, the role of traits of individual species and functional groups in these processes is not well understood as yet. It is recognized that clonality increases the utilization of nutrients, resulting in larger ramet numbers (Jónsdóttir et al., 1996). But patterns of response of individual vegetatively propagating species to alteration of various nutrients still remain understudied.

In grasslands, fertilization often leads to a decrease in species number caused by increased light competition (Cornwell and Grubb, 2003). Gough et al. (2000) found that, overall, the pattern of species-density decrease after fertilization is not clearly related to initial productivity of the site. Callaway et al. (2002) suggested that, owing to the harsh environment, positive interactions among plants play a very important role in alpine environments, whereas light competition is of minor importance, because an individual plant or ramet has a lot of space aboveground. Thus, one can expect that a release from nutrient limitation in alpine environments will cause an increase of biomass without a decrease of community species number. However, only few investigations (e.g., Theodose and Bowman, 1997) tried to check this prediction via an experiment. In the study at Niwot Ridge in the Rocky Mountains, Theodose and Bowman (1997) found that dry and wet communities showed opposite diversity responses to fertilization.

The aim of this study was to examine the response of an alpine lichen heath plant community to an increase in soil-nutrient and water availability induced by fertilization and irrigation. We examined the responses of the total vascular plant community, individual species, and functional groups to nitrogen, phosphorus, nitrogen + phosphorus, calcium, and water additions. Tilman (1982) maintained that plant communities on poor soils are more strongly affected by changes in nutrient availability than those growing on rich soils. Alpine lichen heath plants occur on nutrient-poor soils (Grishina et al., 1993) and, therefore, provide a good environment for such an investigation. We ran a 5-yr (1998–2002) nutrient addition and irrigation experiment on an alpine lichen heath plant community so that we could address the following questions: How is community plant density and flowering influenced by increased nutrient and water availability? How do individual species respond to increased nutrient and water availability? Do clonal and nonclonal species differ in their response to the fertilization and irrigation? How is community diversity and species number influenced by soil-nutrient and water availability?

Study Site and Methods

STUDY SITE

The research was conducted at the Teberda Biosphere Reserve (northwestern Caucasus, Russia). The experimental site was within an alpine lichen heath plant community on the south slope of Mount Malaya Khatipara (43°27′N, 41°42′E at ~2800 m above sea level).

1523-0430/05 $7.00

In the alpine zone of the Caucasus Mountains, alpine lichen heath plant communities are typically situated on south-facing, windward crests and slopes (Onipchenko, 1994). The climate of the area is characterized by low air temperatures (mean annual temperature at the study site is −1.2°C, and mean July temperature is 7.9°C) and high wind velocities (Grishina et al., 1986). Annual precipitation at the study site is high (1400 mm), although the majority falls as snow. Because of the site's position on a windward slope, most of the snow is blown away. Therefore, summer water shortage and deep winter frost are typical of the soil. The soil humus layer is thin (15–20 cm) and contains many stones. The soils are acid ($pH_{KCl} = 4.0$) and relatively poor (available N [determined as NH_4] in the upper soil layer is 120 mg g^{-1}; available P is 60 mg g^{-1}) (Onipchenko, 1994).

The plant community is dominated by fruticose lichens (mainly *Cetraria islandica*), which cover ~50–60% of the area. Vascular plants are represented by >40 species, the most common of which are *Anemone speciosa*, *Antennaria dioica*, *Campanula tridentata*, *Carex sempervirens*, *Carex umbrosa*, *Festuca ovina*, *Trifolium polyphyllum*, and *Vaccinium vitis-idaea* (nomenclature after Vorob'eva and Onipchenko, 2001). Aboveground vascular plant cover is not continuous but rather consists of patches of isolated vascular plants surrounded by lichen areas. The typical size of lichen or vascular plant patches is ~5–10 cm across. For detailed descriptions of the site's plant community, see Onipchenko (1994) and Onipchenko (2002).

EXPERIMENTAL DESIGN AND SAMPLING

The study was conducted during a 5-yr period from 1998 until 2002. The experiment included five treatments: Ca addition (in order to raise soil pH), P, N, and N + P additions, and irrigation. A visually homogeneous area of 19 × 6.5 m was selected on the site and divided into 24 plots. Each plot was 1.5 × 1.5 m; 1-m buffer zones separate plots. The plots were randomly assigned to the treatments, each of which was replicated four times. Within each plot, the numbers of plants per species were counted on a subplot of 0.25 m × 1.0 m, situated at the bottom of the plot. The numbers of generative shoots per species were counted within another subplot of 1.5 m × 0.5 m, situated at the top of each plot.

During the first experimental year (1998), no treatment was applied to the experimental plots, but initial plant abundance was obtained. In 1999, Ca, N, P, and N + P fertilization treatments were started. Calcium was added as lime (52 g lime m^{-2} yr^{-1}) only in 1999 and in 2002. N, P and N + P plots were fertilized annually once a year at the beginning of each growing season. Nitrogen added was in the form of urea (9 g N m^{-2} yr^{-1}); phosphorus added was in the form of double superphosphate (2.5 g P m^{-2} yr^{-1}). Irrigation was conducted in 1999–2002 during the vegetation period (July–August). The mean daily value of evapotranspiration in the area is ~3 mm (Grishina et al., 1986). Every day the precipitation was measured. If the precipitation over a 3-day period did not compensate for the water loss due to evapotranspiration, the plots were irrigated.

Plants and generative shoots were counted by species once a year at the end of July, in the middle of the growing season. In this paper we define "plant" as an individual tiller for graminoids, individual ramet for clonal forbs, or individual rosette for rosette and semirosette forbs. By the term "generative shoot," we mean individual flowering shoots. The counting was done for all the vascular species found on the plots (Appendix 1). It was impossible to distinguish vegetative tillers of *Carex caryophyllea*, *Carex sempervirens*, and *Carex umbrosa* in situ. Therefore, these species were analyzed together as one group, further referred as *Carex* spp.

DATA ANALYSIS

All the statistical analyses—except for the analysis of changes in biodiversity—were done in the same way twice, once for a change in total number of plants and once for a change in number of generative shoots. The statistical analyses performed for changes in the total number of plants and for changes in the number of generative shoots were done through the use of exactly the same methods. To refrain from repetition we therefore only describe the analysis methods for changes in plant numbers.

Community-Level Response and Response of Individual Species

The response of the plant community to the experimental treatments was analyzed by repeated-measures ANCOVA (ANCOVA is analysis of covariance). The observations in 1998 were treated as the covariate. Treatments were the between-subject factor, the year was the within-subject (repeated) factor, and the total number of plants (which was obtained by summing the number of plants through all species per plot) was a response variable. The null hypothesis was that during the years 1999–2002, there were no differences between treatments in the number of plants, adjusted for the number of plants in the year before treatment (i.e., in 1998). If the ANCOVA showed that the effect of the treatment was significant, an ANCOVA with planned contrasts against the controls was done. Although such contrasts were not orthogonal, we relied on the approach of Quinn and Keough (2002), who noted that when contrasts represent independent hypotheses, no multiple testing is involved and therefore the risk of family-wise type I error is not considerably increased.

Because this analysis indicated that the plant density per plot was influenced by the experimental treatments, the two-way repeated-measures ANCOVA was done with the treatment and species as independent variables, the year as a repeated factor, and the number of plants as a response variable. The null hypothesis was that for a given amount of density increase, all species would increase their abundance proportionally. Because we found that species differed in their response to treatment, the response of individual species was analyzed. Changes in the number of plants for individual species were analyzed in the same way as changes in the plant number of the total community.

Graminoids vs. Forbs and Clonal vs. Nonclonal Species

The numbers of all the graminoids and forbs were separately summed per plot. Thus, the total number of graminoid and the total number of forb plants were obtained for each plot. The data were subjected to a two-way repeated-measures nested ANCOVA that regarded growth form and treatment as between-subject factors, the year as a within-subject (repeated) factor, the numbers of graminoid or forb plants per plot as a response variable, and the respective numbers of graminoid or forb plants on a plot in 1998 as a covariate. The null hypothesis stated that the response of graminoids and forbs to treatments were the same (i.e., during the years when the treatments were applied, there was no difference between forbs and graminoids in the number of plants between treatments).

Because the ANCOVA showed that interaction between species type and treatment was significant, a separate repeated-measures ANCOVA was performed for graminoids and forbs. If significant, for each treatment the mean value was compared with the control mean by running a repeated-measures ANCOVA with respective planned contrasts.

To analyze the role of clonality we divided all species into two groups: clonal and nonclonal (Appendix 1). This division is arbitrary, because as Jónsdóttir et al. (1996) noted, most of the species are clonal to some extent and in reality we are rather dealing with a gradient of clonality than with two separate groups. For the purposes of our analysis, we defined "clonal plants" as plants that maintain persistent ramet connections. The statistical analysis of the role of clonality was done in the same way as the analysis of graminoids vs. forbs already described.

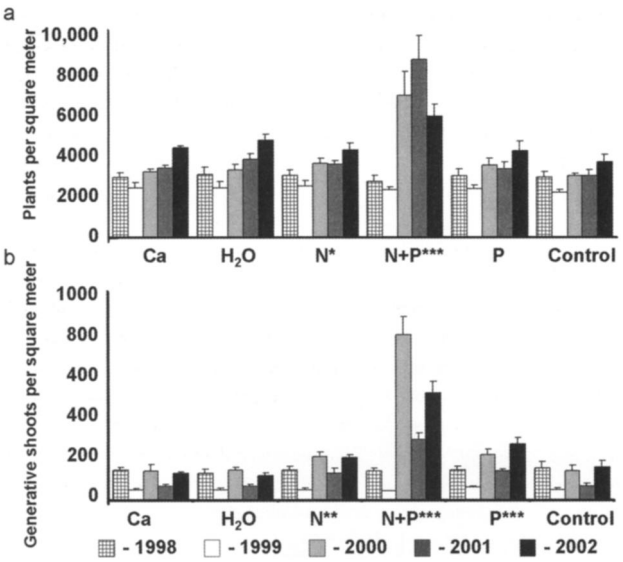

FIGURE 1. Annual (1998–2002) changes in plant density (number of plants per square meter) and number of generative shoots per square meter as influenced by experimental treatments over the period 1999–2002. Error bars represent standard errors ($n = 4$) of mean values calculated for 1 yr. Asterisks represent a significance of difference between mean values of the number of plants (or the number of generative shoots) at the labeled treatment and control, as analyzed via repeated-measures ANCOVA with planned contrasts. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

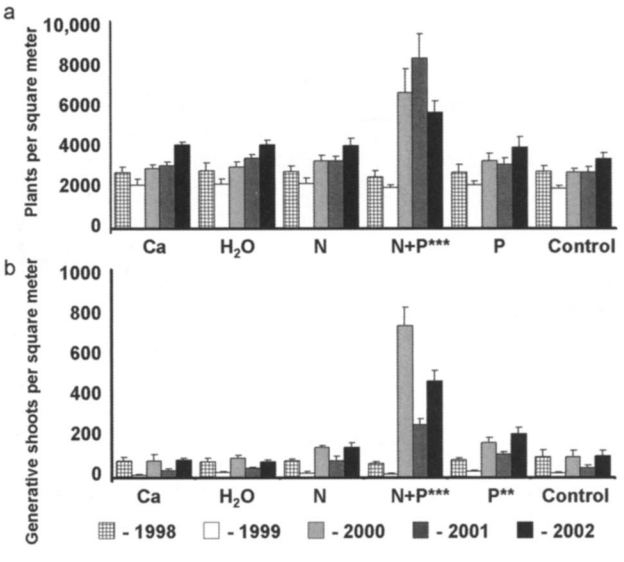

FIGURE 2. Annual (1998–2002) changes in clonal plant density (number of plants per square meter) and number of generative shoots per square meter as influenced by experimental treatments over the period 1999–2002. Error bars represents standard errors ($n = 4$) of mean values calculated for one year. Asterisks represent a significance of difference between mean values of number of plants (or a number of generative shoots) at respective treatment and control analyzed via repeated-measures ANCOVA with planned contrasts. **$P < 0.01$, ***$P < 0.001$.

Changes in Biodiversity

We counted the species numbers on the 0.25 m × 1.0 m plots, where numbers of plants were counted. Subsequently, the Shannon-Wiener diversity coefficient—based on plant number per species—was calculated for every plot. Statistically, these data were analyzed in the same way as the data of response of individual species.

Assumptions of the Statistical Analyses

Normality of population distributions was tested with the Kolmogorov-Smirnov test, and variance homogeneity was tested with the Levene test and with graphical checks of residual spreads plotted against group means. Log, square-root, or cubic-root transformation of the data was applied were necessary. The assumption of homogeneity of within-group regression slopes, which is necessary for ANCOVA, was checked by running an ANOVA (analysis of variance) test with treatment as the between-subject factor, plot nested within treatment as a random factor, year as a within-subject factor, and the interaction between treatment and 1998 observations as a test of the null hypothesis of equal slopes (Quinn and Keough, 2002).

Results

Changes in the plant community appeared at the second year of fertilization. In the result descriptions we mention values of increase or decrease averaged over the three last experimental years.

The total number of plants and the number of generative shoots (Fig. 1) were strongly influenced by treatments ($P < 0.001$ in both cases). The total number of plants increased ~400% in response to N + P treatment ($P < 0.001$) and showed a slight, marginally significant increase in response to H_2O and N treatments (120% in both cases, $P = 0.065$ and $P = 0.045$, respectively). The number of generative shoots increased ~400% in N + P plots ($P < 0.001$) and slightly but significantly increased in N (150%, $P = 0.005$) and P (170%, $P < 0.001$) plots.

Forbs differed from graminoids in their response to treatments, considering the total number of plants as well as the number of generative shoots ($P < 0.001$ in both cases). The total numbers of forb plants per plot were not influenced by treatments, while the total number of graminoids increased 20% in response to P treatment ($P = 0.028$) and threefold in response to N + P treatment . The number of forb generative shoots doubled in N plots ($P = 0.002$) and increased 1.5 times in N + P plots; the latter result was, however, only marginally significant ($P = 0.065$). The number of graminoid generative shoots increased by a factor of 10 in response to N + P treatment ($P < 0.001$) and by a factor of 3.5 in response to P treatment ($P = 0.002$). Patterns of change in number of plants and change in number of generative shoots induced by experimental treatments varied strongly between species (Appendixes 2 and 3).

An ANOVA showed that interaction between clonality and treatment was significant both for the number of plants and for the number of generative shoots ($P < 0.001$ in both cases), suggesting that clonal and nonclonal plants respond differently to at least some treatments. Clonal species increased the total number of plants in response to N + P treatments ($P < 0.001$) and the number of generative shoots in response to N + P and P treatments (Fig. 2). Nonclonal species did not show any significant response to the treatments (data not shown).

Species number ranged between 20 and 23 per plot and was not affected by any of the treatments. The Shannon-Wiener diversity, however, decreased in response to N + P treatment during the last three years of the experiment (Fig. 3). The decrease was 30%, 35%, and 18%, in the years 2000, 2001, and 2002, respectively.

Discussion

RESPONSE TO NITROGEN AND PHOSPHORUS ADDITIONS

Our experiment has demonstrated the importance of nutrient limitations for the composition of an alpine lichen heath plant community. Körner (2003) suggested that in many parts of the world, productivity of alpine plants is limited mostly by nitrogen. Our results

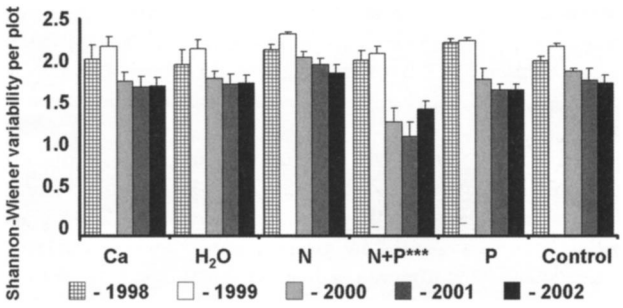

FIGURE 3. Annual (1998–2002) changes in values of Shannon-Wiener index per 0.25 m^2 plot as influenced by experimental treatments over the period 1999–2002. Error bars represents standard errors ($n = 4$) of mean values calculated for one year. Asterisks represent a significance of difference between mean values of Shannon-Wiener index at respective treatment vs. control analyzed via repeated-measures ANCOVA with planned contrasts. ***$P < 0.001$.

indicate that in the Caucasus, a second limiting factor might be phosphorus. This finding is consistent with data showing a low concentration of soil phosphorus at the experimental site (Makarov, 1995; Vertelina et al., 1996). Addition of nitrogen and phosphorus together caused the strongest positive response, both in number of plants and number of generative shoots, indicating that these nutrients are co-limiting productivity on the site. Remarkably, there were no clear annual trends in any of the responses to treatments.

Overall plant density strongly increased after N + P additions and slightly increased after N additions. However, the total number of forbs plants was not affected by the experimental treatments. Thus, the shift in total plant number was caused mostly by an increase in the number of graminoid plants. Nevertheless, many forbs responded (although not always to a statistically significant degree) to N and N + P treatments by an increase in the number of generative shoots. This finding is in agreement with the work of Castro-Díez et al. (2003), who suggested that plant growth can follow one of two strategies: allocation most of available resources to seed production or to vegetative growth.

All graminoids increased their abundance in response to N + P treatment. This finding is consistent with results obtained in similar experiments (e.g., Jonasson, 1992; Press et al., 1998a; Turkington et al., 1998). The response to additions of only nitrogen or phosphorus, however, varied between graminoid species. Thus, the N + P co-limitation of graminoids is rather a result of a coexistence of N- and P-limited species within the community, than an overall pattern.

Similar to previous reports (Jeffrey, 1971; Rosén, 1982; Pop and Resmerita, 1988), *Festuca ovina* responded positively to N + P fertilization. However, this species, which is known as stress tolerant (Grime, 1977), but a bad competitor in richer soils (Grime, 1977; Austin and Austin, 1980), decreased plant number and the number of generative shoots during N treatment. *Helictotrichon versicolor* showed the same pattern. Bohmer (1994) claimed that *Helictotrichon versicolor* prefers rich soils. Our results show that this species, nevertheless, lost to other species in competition for soil nutrients, when nitrogen fertilizer was applied.

Three *Carex* species found at the site were analyzed together as one group. This approach might have led to some misinterpretation of the results, as *Carex* species can vary in their nutrient requirements (Henry et al., 1986; Aerts and De Caluwe, 1994). Gigon (1971) claimed that *Carex sempervirens* does not show a positive response to nitrogen fertilizers. Henry et al. (1986) reported that *Carex* species responded positively only to N + P + K fertilizer, but did not show any response to addition of nitrogen only. In contrast to these findings, our results demonstrate that *Carex* spp. was the only graminoid that responded positively to addition of nitrogen only and even possibly caused a decrease of other graminoids on these plots. Grime (2001) stressed the importance of cluster roots that increase the capacity of certain sedges for phosphorus scavenging and uptake. In line with this claim, in our experiment the number of *Carex* plants decreased after phosphorus fertilization, suggesting little limitation by phosphorus for *Carex*. At the same time, *Festuca ovina* increased its abundance and the number of generative shoots in response to phosphorus additions. This finding is consistent with data presented by Tyler (1996), who reported that the abundance of *F. ovina* is positively correlated with the availability of exchangeable soil phosphates. These facts suggest that the changes in soil-nutrient availability induced an alteration of the competitive balance between the *Carex* species and *F. ovina* (Tilman and Wedin, 1991; Hartley and Amos, 1999). These two species are the most abundant at the site. Our data demonstrate that on phosphorus-fertilized plots, *Festuca ovina* possibly became a stronger competitor than *Carex* and caused the decrease of the latter, whereas *Carex* benefited more from nitrogen.

RESPONSE TO CALCIUM ADDITION

It has been demonstrated that pH level can influence uptake of nitrogen and phosphorus from soil and therefore plant performance (Tilman and Olff, 1991; Tyler, 1994). Shatvorjan (1977) reported that calcium additions increased biomass production on a grassland with a relatively low soil pH (4.7 in the deep soil layer, 5.5 in the upper soil layer). These results suggest that at lower soil pH, some species may benefit from calcium additions. Although at our site the soil properties are comparable with those in the work of Shatvorjan (1977), our results show that calcium fertilization did not cause a considerable change in the plant community. Only *Festuca ovina* increased its plants number unequivocally during the calcium-addition experiment, but the magnitude of the increase was not high in comparison with the control.

RESPONSE TO IRRIGATION

It has been demonstrated (see reviews of Oberbauer and Dawson [1992] and Callagan and Jonasson [1995]) that plant communities of the High Arctic, which grow in somewhat similar conditions and are often compared to those of alpine tundra, are often limited by water availability. Our results suggest that the majority of alpine heath plants are well adapted to the natural water shortage. Similar results of absence of response to irrigation were reported by Bowman et al. (1995) for an alpine tundra plant community on Niwot Ridge of the Colorado Rocky Mountains.

The only species that increased its number of plants sharply, even 10-fold, in irrigated plots was the annual *Euphrasia ossica*. *Euphrasia ossica* is a hemiparasitic species (Michelsen et al., 1998), but at early stages it obtains water and nutrients from soil and depends therefore on soil humidity. Like most hemiparasitic species, it has a high transpiration rate (Press et al., 1998b). Because of this, it is probably strongly affected by summer droughts. Release from water shortage, therefore, caused a major increase in number of plants. This finding is consistent with that of Grubb (1983), who claimed that a morphologically close species, *Euphrasia officinalis*, is very sensitive to drought in meadows of south England.

Among perennials, only *Festuca ovina* increased its abundance in response to irrigation, but the magnitude of the increase was not large in comparison with controls. *Vaccinium vitis-idaea* did not show any response to irrigation. In a similar experiment in the subarctic, *Vaccinium vitis-idaea* responded idiosyncratically. Shevtsova et al. (1997) reported that it increased the growth rate in response to irrigation, whereas in experiment of Press et al. (1998a), it did not respond to additional water supply.

CORRELATION WITH ROOT DEPTHS

It is commonly agreed that root properties play an important role in the mineral nutrition of plants (Chapin, 1980). In our experiment, changes in total plant number in response to treatments closely correlated with the root depth of the species. The data about species' root systems was adopted from the work of Onipchenko (1987). Deep-rooted *Trifolium polyphyllum* and *Arenaria lychnidea* (roots penetrate deeper than 15 cm) responded only to nitrogen treatment, whereas species with intermediate and shallow root systems (*Alchemilla caucasica*, *Carex* spp., *Festuca ovina*, *Helictotrichon versicolor*, *Luzula spicata*) also showed pronounced response to phosphorus additions (P and/or N + P treatments). This difference probably occurred because the added phosphorus did not penetrate into deep soil layers. Species with shallow root systems (roots do not penetrate deeper than 5 cm), such as *Festuca ovina* and *Euphrasia ossica*, are probably strongly influenced by droughts and therefore responded positively to irrigation. The changes in number of generative shoots induced by fertilization did not have any correlation with root depth of plants.

CLONAL VS. NONCLONAL SPECIES

Several studies have shown that clonality improves the efficiency of nutrient use (Headly et al., 1988; Jónsdóttir and Callagan, 1988) and nutrient scavenging (De Kroon and Van Groenendael, 1997). As the physiological adaptations for efficient nutrient use, rather than for efficient nutrient uptake, are of greater importance in poor soils (Chapin, 1980), it would be logical to expect that clonal species would benefit more from nutrient additions than nonclonal species. Our results confirm this assumption. The analysis of individual species demonstrated that, except for *Euphrasia ossica*, only clonal species increased their abundance significantly. Considered as a group, nonclonal species did not respond to any experimental treatment. A possible explanation for such a response pattern could be that seedling establishment, which is critical for nonclonal species, is more difficult in the dense cover after fertilization. However, the analysis of the response of clonal species indicated that this group increased its density only in response to N + P treatment, whereas the total community density increased in response to N + P and N treatments. Similarly, the number of generative shoots of clonal species increased in response to N + P and P treatments, whereas the number of generative shoots of the total community increased in response to N, N + P, and P treatments. This result suggests that it was the group of nonclonal species that made a positive response to N treatment in both cases.

CHANGES IN BIODIVERSITY AND SPECIES RICHNESS

Increased availability of limiting nutrients often leads to increase in community productivity and reduction of diversity (Tilman, 1982; Elisseou et al., 1995; Grime, 2001). Although nitrogen additions slightly increased the productivity of our site, this increase tended to be proportional for the site species and therefore did not result in changes of vegetation diversity. In contrast, addition of nitrogen and phosphorus together caused a disproportionate increase in plant numbers of several species. This result suggests an increase in competitive interactions caused by the increase in availability of this nutrient (Grime, 1973). However, similar to the findings of Elisseou et al. (1995) and Kalmbacher and Martin (1996), the addition of phosphorus alone did not change the vegetation diversity. It is, nevertheless, important to realize that changes in shoot number do not necessary lead to changes in biomass. The question, whether a response of the community biomass follows a similar pattern, stays open for future research.

In recent years many researchers sought the evidence that species richness changes with the increase in nutrient availability, resulting in an increase in community productivity. However, the results reported are contradictory. Some authors (Willems et al., 1993; Chapin, 1995; Molau and Alatalo, 1998; Aerts et al., 2003) have demonstrated a decrease in species number caused by an increase in soil-nutrient availability, whereas others (Jonasson, 1992; Bowman et al., 1993; Huber, 1994) reported an absence of significant changes or even an increase in the number of species.

Grime (2001) stressed the importance of competition for light for the process of local species extinction caused by increased biomass. However, the hump-shaped relationship between productivity and species richness suggested by Grime has not always been found (Waide et al., 1999; Cornwell and Grubb, 2003) especially when the observations were conducted at small plots (Oksanen, 1996; Gross et al., 2000). When such a relationship is observed, the location of the hump in the hump-shaped curve depends on many biotic and abiotic factors such as type of plant community and availability of soil nutrients and water (Cornwell and Grubb, 2003).

Although Cornwell and Grubb (2003) showed that for grassland species, richness peaks occur on poor nutrient soils, decreasing with fertilization, they questioned the generality of this pattern for all types of plant community. It is suggested that in communities in which an individual plant has a lot of space aboveground (we consider the plant community in this study to be of this type), light competition does not play an important role and does not lead to species' die-off even when the productivity increases. Similarly, Jonasson (1992) suggested that tendencies in the changes of the number of species depend not only on nutrient availability but also on the rate of competitive exclusion. If this rate stays low, then the number of species does not decline under fertilization. In line with this theory, the number of species in our experiment did not change significantly under any of the experimental treatment. Another important factor is that most of the species analyzed within the experiment are perennials and therefore might have resources to survive for several years under unfavorable conditions. Thus, considerable changes in species number might take longer than 4 yr.

Several researchers have demonstrated that, in contradiction to nutrients, increased water availability does not lead to decrease in species number, caused by increase in productivity, but rather leads to increase in species number or does not cause any changes in species richness (Sarmiento, 1983; Goldberg and Miller, 1990; Jobbágy et al., 1996). Cornwell and Grubb (2003) suggested that water limitation is a more stochastic factor than nutrient limitation and therefore it more often causes extinction of species. Thus, release from water shortage should increase rather than decrease the species number. This explanation is applicable to our results. We found that irrigation did not decrease the number of species and the relatively short time of the experiment was not enough for new species to establish.

Conclusions

In exploring the mechanisms of nutrient and water limitations of the alpine lichen heath plant community in the northwestern Caucasus, this work has revealed interesting features of individual species as well as species groups. We showed that the plant community is co-limited by nitrogen and phosphorus. The experiments also demonstrated that even though the conditions are normally dry, irrigation did not cause changes in plant numbers for most of the species. Addition of nitrogen in combination with phosphorus caused a considerable decrease in the community diversity as suggested by the disproportionate changes in plant number of several species. Future work is to be aimed at further exploration of the physiological issues of nutrient cycling in the community, such as nutrient concentration in plant tissues, nutrient absorption and resorption, and changes in biomass.

Acknowledgments

We are very grateful to Alexei Zakharov and Nikita Tiunov for their help with irrigation. We would like to take this opportunity to

thank Hans Cornelissen, Rien Aerts, and Peter Bogedom for their helpful comments and discussions. Our thanks are also due to the Russian Foundation for Fundamental Research for financial support of this research (project NN 05-04-48578).

References Cited

Aerts, R., and De Caluwe, H., 1994: Nitrogen use efficiency of *Carex* species in relation to nitrogen supply. *Ecology,* 75: 2362–2372.

Aerts, R., De Caluwe, H., and Beltman, B., 2003: Is the relation between nutrient supply and biodiversity co-determined by the type of nutrient limitation. *Oikos,* 101: 489–498.

Austin, M. P., and Austin, B. O., 1980: Behavior of experimental plant community along a nutrient gradient. *Journal of Ecology,* 68: 891–918.

Billings, W. D., 1974: Arctic and alpine vegetation: Plant adaptations to cold summer climates. *In* Ives, J. D., and Barry, R. G. (eds.), *Arctic and alpine environments.* New York: Methuen, 403–443.

Bohmer, H. J., 1994: Struktur und Dynamik des alpinen Krummseggengrasens im Spiegel der Mosaik-Zyklus-Theorie. *Geoökodynamik,* 15: 89–103.

Bowman, W. D., and Fisk, M. C., 2001: Primary production. *In* Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and function of an alpine ecosystem.* Oxford: Oxford University Press, 169–197.

Bowman, W. D., Theodose, T. A., Schardt, J. C., and Conant, R. T., 1993: Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology,* 74: 2085–2097.

Bowman, W. D., Theodose, T. A., and Fisk, M. C., 1995: Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: Implications for differential community response to environmental change. *Oecologia,* 101: 217–227.

Callagan, T. V., and Jonasson, S., 1995: Implications for changes in Arctic plant biodiversity from environmental manipulation experiments. *In* Chapin, F. S., III, Shaver, G. R. (eds.), *Arctic and alpine biodiversity. Ecological Studies,* 113: 150–166.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., and Cook, B. J., 2002: Positive interactions among alpine plants increase with stress. *Nature,* 407: 844–847.

Castro-Díez, P., Montserrat-Martí, G., and Cornelissen, J. H. C., 2003: Trade-offs between phenology, relative growth rate, life form and seed mass among 22 Mediterranean woody species. *Plant Ecology,* 166: 117–129.

Chapin, F. S., III, 1980: The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics,* 11: 233–260.

Chapin, F. S., III, 1995: Responses of arctic tundra to experimental and observed changes in climate. *Ecology,* 76: 694–711.

Chapin, F. S., III, and Shaver, G. R., 1985: Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology,* 66: 564–576.

Cornwell, W. K., and Grubb, P. J., 2003: Regional and local patterns in plant species richness with respect to resource availability. *Oikos,* 100: 417–428.

De Kroon, H., and Van Groenendael, J. M., 1997: *The ecology and evolution of clonal growth in plants.* Leiden: Backhuys Publishers, 456 pp.

Elisseou, G. C., Veresoglou, D. S., and Mamolos, A. P., 1995: Vegetation productivity and diversity of acid grasslands in northern Greece as influenced by winter rainfall and limiting nutrients. *Acta Ecologia,* 16: 687–702.

Fisk, M. C., Schmidt, S. K., and Seastedt, T. R., 1998: Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology,* 79: 2253–2266.

Gigon, A., 1971: *Vergleich alpiner Rasen auf Silikat- und auf Karbonatboden.* Zürich: Stiftung Rübel, Veröffentlichungen des Geobotanischen Institutes der ETH, Heft 48, 159 pp.

Goldberg, D. E., and Miller, T. E., 1990: Effects of different resource additions on species diversity in an annual plant community. *Ecology,* 71: 213–225.

Gough, L., Osenberg, C. W., Gross, K. L., and Collins, S. L., 2000: Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos,* 89: 428–439.

Grime, J. P., 1973: Competitive exclusion in herbaceous vegetation. *Nature,* 242: 334–347.

Grime, J. P., 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist,* 982: 1169–1194.

Grime, J. P., 2001: *Plant strategies, vegetation processes, and ecosystem properties.* 2nd ed. Chichester: John Wiley and Sons, 417 pp.

Grishina, L. A., Onipchenko, V. G., and Makarov, M. I., 1986: *Composition and structure of alpine heath biogeocoenosis.* Moscow: Izd-vo Moskovskogo Universiteta, 88 pp. (In Russian.)

Grishina, L. A., Onipchenko, V. G., Makarov, M. I., and Vanyasin, V. A., 1993: Changes in properties of mountain-meadow alpine soils of the northwestern Caucasus under different ecological conditions. *Eurasian Soil Science,* 25: 1–12.

Gross, K. L., Willig, M. R., Gough, L., Inouye, R., and Cox, S. B., 2000: Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos,* 89: 417–427.

Grubb, P. J., 1983: Some growth points in investigative plant ecology. *In Trends in Ecological Research 1980. Proceedings, NATO ARW and INTECOL Workshop Future and Use Ecological Decado Environment, Louvain-la-Neuve, 1–9 April, 1983,*51–74.

Hartley, S. E., and Amos, L., 1999: Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: The effect of fertilizer and defoliation on above- and below-ground performance. *Journal of Ecology,* 87: 330–340.

Headly, A. D., Callagan, T. V., and Lee, J. A., 1988: Phosphate and nitrate movement in the clonal plants *Lycopodium annotinum* L. and *Diphasiastrum complanatum* (L.) Holub. *New Phytologist,* 110: 497–502.

Henry, G. H. R., Freedman, B., and Svoboda, J., 1986: Effects of fertilization on three tundra plant communities of a polar desert oasis. *Canadian Journal of Botany,* 64: 2502–2507.

Huber, R., 1994: Changes in plant species richness in a calcareous grassland following changes in environmental conditions. *Folia Geobotanica et Phytotaxonomica, Praha,* 29: 469–482.

Jeffrey, D. W., 1971: The experimental alteration of a *Kobresia*-rich sward in Upper Teesdale. *In* Dufley, E., and Watt, A. S. (eds.), *The scientific management of animal and plant communities for conservation. The 11th Symposium of the British Ecological Society, University of East Anglia, Norwich, 7–9 July 1970.* Oxford: Blackwell Scientific Publications, 79–89.

Jobbágy, E. G., Paruelo, J. M., and León, R. J. C., 1996: Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina). *Journal of Vegetation Science,* 7: 599–608.

Jonasson, S., 1992: Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos,* 63: 420–429.

Jónsdóttir, I. S., and Callagan, T. V., 1988: Interrelations between different generations of interconnected tillers of Carex bigelowii. *Oikos,* 52: 120–128.

Jónsdóttir, I. S., Callaghan, T. V., and Headley, A. D., 1996: Resource dynamics within arctic clonal plants. *Ecological Bulletins,* 45: 53–64.

Kalmbacher, R., and Martin, F., 1996: Shifts in botanical composition of flatwoods range following fertilization. *Journal of Range Management,* 49: 530–534.

Körner, C., 2003: *Alpine plant life: Functional plant ecology of high mountain ecosystems,* 2nd ed. Berlin: Springer, 344 pp.

Makarov, M. I., 1995: Phosphorus status of humic acids in mountain soils of the north-western Caucasus. *Vestnik Moskovskogo Universiteta, seria 17, Pochvovedenie,* 1: 38–48. (In Russian.)

Marschner, H., 2002: *Mineral nitration of higher plants.* 2nd ed. London: Academic Press, 889 pp.

Michelsen, A., Quarmby, C., Sleep, D., and Jonasson, S., 1998: Vascular plant N^{15} natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia,* 115: 406–418.

Molau, U., and Alatalo, J. M., 1998: Responses of subarctic-alpine plant communities to simulated environmental change: Biodiversity of bryophytes, lichens, and vascular plants. *Ambio,* 27: 322–329.

Oberbauer, S. F., and Dawson, T. E., 1992: Water relations of arctic vascular plants. *In* Chapin, F. S., III, Jerries, R. L., and Reynolds, J. F. (eds.), *Arctic ecosystems in a changing climate.* San Diego, California: Academic Press, 259–279.

Oksanen, J., 1996: Is the humped relationship between species richness and biomass an artefact due to plot size?. *Journal of Ecology,* 84: 293–295.

Onipchenko, V. G., 1987: Mechanisms of ecological niches separation in terrestrial plants. *Zhurnal obshchei biologii,* 48: 687–695. (In Russian.)

Onipchenko, V. G., 1994: Study area and general description of the investigated communities. *In* Onipchenko, V. G., and Blinnikov, M. S., (eds.), *Experimental investigation of alpine plant communities in the northwestern Caucasus.* Zürich: Stiftung Rübel, Veröffentlichungen des Geobotanischen Institutes der ETH, 115: 6–22.

Onipchenko, V. G., 2002: *Alpine vegetation of the Teberda Reserve, the northwestern Caucasus.* Zürich: Stiftung Rübel, Veröffentlichungen des Geobotanischen Institutes der ETH, Heft 130, 168 pp.

Pop, I., and Resmerita, I., 1988: Phytocenological evaluation of trophicity of grassland soils in the Romanian Carpathians. *Studia Universitatis Babes—Bolyai, Biologia,* 33: 3–8.

Press, M. C., Potter, J. A., Burke, M. J. W., Callaghan, T. V., and Lee, J. A., 1998a: Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology,* 86: 315–327.

Press, M. C., Scholes, J. D., and Watling, J. R., 1998b: Parasitic plants physiological and ecological interactions with their hosts. *In* Press, M. C. (ed.), *Physiological Plant Ecology: The 39th Symposium of the British Ecological Society, held at the University of York, 7–9 September 1998.* Cambridge, Cambridge University Press, 175–198.

Quinn, G., and Keough, M., 2002: *Experimental design and data analysis for biologists.* Cambridge: Cambridge University Press, 537 pp.

Rosén, E., 1982: Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. *Acta Phytogeographica Suecica,* 72: 108.

Sarmiento, G., 1983: Patterns of specific and phenological diversity in the grass community of the Venezuelan tropical savannas. *Journal of Biogeography,* 10: 373–391.

Seastedt, T. R., and Vaccaro, L., 2001: Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research,* 33: 100–106.

Shatvorjan, P. V., 1977: Influence of liming on after-forest grassland productivity. *In Materialy nauchnoy sessii po itogam issledovatelskikh rabot Armyanskogo nauchno-issledovatel'skogo instituta. Zhivotnovodstva i Veterinarii,* 25–28.11.1977. Erevan: Aystan, 111–113. (In Russian.)

Shaver, G. R., and Chapin, F. S., III, 1995: Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography,* 18: 259–275.

Shevtsova, A., Haukioja, E., and Ojala, A., 1997: Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated environmental conditions and species removal. *Oikos,* 78: 440–458.

Theodose, T. A., and Bowman, W. D., 1997: Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology,* 78: 1861–1872.

Tilman, D., 1982: *Resource competition and community structure.* Princeton, New Jersey: Princeton University Press, 296 pp.

Tilman, D., and Olff, H., 1991: An experimental study of the effects of pH and nitrogen on grassland vegetation. *Acta Oecologia,* 12: 427–441.

Tilman, D., and Wedin, D., 1991: Dynamics of nitrogen competition between successional grasses. *Ecology,* 72: 1038–1049.

Turkington, R., John, E., Krebs, C. J., Dale, M. R. T., Nams, V. O., Boonstra, R., Boutin, S., Martin, K., Sinclair, A. R. E., and Smith, J. N. M., 1998: The effects of NPK fertilization for nine years on boreal forest vegetation in northwestern Canada. *Journal of Vegetation Science,* 9: 333–346.

Tyler, G., 1994: A new approach to understanding the calcifuge habit of plants. *Annals of Botany,* 73: 327–330.

Tyler, G., 1996: Cover distributions of vascular plants in relation to soil chemistry and soil depth in a granite rock ecosystem. *Vegetatio,* 127: 215–223.

Vertelina, O. V., Onipchenko, V. G., and Makarov, M. I., 1996: Primary minerals and processes of weathering in high-mountain soils of the Teberda Reserve. Vestnik Moskovskogo Universiteta, *seria 17, Pochvovedenie,* 51: 1–8. (In Russian.)

Vorob'eva, F. M., and Onipchenko, V. G., 2001: Vascular plants of Teberda Reserve. *Flora i fauna zapovednikov.* Moscow, 99: 1–100. (In Russian.)

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., and Parmenter, R., 1999: The relationship between productivity and species richness. *Annual Review of Ecology and Systematics,* 30: 257–300.

Walker, M. D., Webber, P. J., Arnold, E. H., and Ebert-May, D., 1994: Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology,* 75: 393–408.

Willems, J. H., Peet, R. K., and Bik, L., 1993: Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science,* 4: 203–212.

Revised ms submitted February 2005

APPENDIX 1

List of species analyzed within the experiment and their clonality features.

Plant	Clonality
Alchemilla caucasica Buser	Clonal
Anemone speciosa Adams ex G. Pritz.	Nonclonal
Antennaria dioica (L.) Gaertn.	Clonal
Arenaria lychnidea Bieb.	Clonal
Aster alpinus L.	Clonal
Campanula collina Bieb.	Clonal
Campanula tridentata Schreb.	Nonclonal
Carex caryophyllea Latourr	Clonal
Carex sempervirens Vill.	Clonal
Carex umbrosa Host	Clonal
Carum caucasicum (Bieb.) Boiss.	Nonclonal
Erigeron alpinus L.	Clonal
Eritrichium caucasicum (Albov) Grossh.	Nonclonal
Euphrasia ossica Juz.	Nonclonal
Festuca ovina L.	Clonal
Fritillaria collina Mill.	Nonclonal
Gentiana aquatica L.	Nonclonal
Gentiana biebersteinii Bunge	Nonclonal
Gentiana pyrenaica L.	Clonal
Gentiana septemfida Pall.	Nonclonal
Gentiana verna L.	Clonal
Helictotrichon versicolor (Vill.) Pilger	Clonal
Lloydia serotina (L.) Reichenb.	Nonclonal
Luzula spicata (L.) DC.	Clonal
Minuartia circassica (Albov) Woronow	Clonal
Minuartia recurva (All.) Schinz et Thellung	Clonal
Oxytropis kubanensis Leskov	Nonclonal
Pedicularis comosa L.	Nonclonal
Plantago atrata Hoppe	Nonclonal
Polygonum bistorta L.	Clonal
Potentilla gelida C. A. Mey.	Clonal
Potentilla nivea L.	Clonal
Primula algida Adams	Clonal
Primula ruprechtii Kusn.	Clonal
Ranunculus oreophilus Bieb.	Clonal
Scorzonera cana (C. A. Mey.) O. Hoffm.	Nonclonal
Taraxacum stevenii DC.	Nonclonal
Trifolium polyphyllum C. A. Mey.	Clonal
Vaccinium vitis-idaea L.	Clonal
Veronica gentianoides Vahl.	Clonal

APPENDIX 2

Annual changes in plant density induced by experimental treatments over the period 1999–2002; 1998 values are used as a control. Mean values of plant number per square meter and their standard errors ($n = 4$) are shown. Data are presented for all the species that showed a significant or a large-magnitude (although statistically not significant [ns]) response to at least one of the treatments. Arrows ↑ and ↓ indicate increase and decrease, respectively. *P* level indicates the significance of difference between mean values of plant numbers at each respective treatment and control analyzed via repeated-measures ANCOVA with planned contrasts.

Species	Treatment	*P* level	1998	1999	2000	2001	2002
Alchemilla caucasica	Ca		27 ± 16	19 ± 11	18 ± 11	25 ± 15	68 ± 40
	H_2O		30 ± 27	28 ± 24	25 ± 24	24 ± 24	23 ± 22
	N		14 ± 10	14 ± 11	18 ± 11	17 ± 13	29 ± 15
	N + P	ns↑	12 ± 9	15 ± 10	33 ± 19	81 ± 49	88 ± 81
	P		5 ± 5	6 ± 5	5 ± 5	3 ± 3	6 ± 6
	Control		36 ± 27	25 ± 16	32 ± 24	36 ± 29	41 ± 34
Arenaria lychnidea	Ca		8 ± 8	16 ± 16	21 ± 21	26 ± 25	18 ± 18
	H_2O		40 ± 40	38 ± 38	49 ± 49	45 ± 45	39 ± 39
	N	ns↑	60 ± 52	196 ± 123	295 ± 164	429 ± 325	582 ± 477
	N + P		17 ± 17	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	P		97 ± 97	92 ± 92	143 ± 116	186 ± 137	162 ± 133
	Control		0 ± 0	14 ± 14	16 ± 16	19 ± 18	27 ± 27
Carex spp.	Ca		266 ± 35	271 ± 42	219 ± 42	267 ± 47	341 ± 101
	H_2O		299 ± 91	232 ± 70	237 ± 109	214 ± 74	269 ± 124
	N	0.002↑	280 ± 39	296 ± 41	591 ± 111	695 ± 181	999 ± 214
	N + P	ns↑	327 ± 26	260 ± 52	477 ± 66	510 ± 81	554 ± 49
	P	ns↓	284 ± 30	283 ± 16	185 ± 29	146 ± 41	178 ± 31
	Control		280 ± 49	279 ± 47	256 ± 48	242 ± 29	263 ± 49
Euphrasia ossica	Ca		21 ± 13	38 ± 25	14 ± 7	29 ± 6	82 ± 54
	H_2O	0.012↑	40 ± 20	24 ± 15	72 ± 20	170 ± 64	426 ± 257
	N		20 ± 8	10 ± 7	35 ± 14	4 ± 0	4 ± 3
	N + P		17 ± 10	18 ± 7	65 ± 16	61 ± 13	31 ± 22
	P		50 ± 16	33 ± 14	24 ± 16	12 ± 7	38 ± 26
	Control		25 ± 7	19 ± 11	34 ± 15	31 ± 19	99 ± 68
Festuca ovina	Ca	0.019↑	827 ± 124	724 ± 91	1483 ± 70	1954 ± 136	2079 ± 139
	H_2O	0.046↑	836 ± 200	664 ± 116	1340 ± 140	2138 ± 284	1878 ± 247
	N	0.034↓	887 ± 70	550 ± 105	1047 ± 219	1121 ± 113	916 ± 145
	N + P	<0.001↑	947 ± 203	929 ± 144	4780 ± 1074	6550 ± 1135	3652 ± 552
	P	0.012↑	767 ± 22	658 ± 50	1682 ± 218	1878 ± 207	2163 ± 183
	Control		914 ± 190	615 ± 85	1101 ± 111	1619 ± 317	1670 ± 479
Helictotrichon versicolor	Ca		96 ± 16	84 ± 10	83 ± 21	109 ± 34	99 ± 28
	H_2O		64 ± 18	59 ± 14	73 ± 20	69 ± 25	76 ± 25
	N	0.011↓	166 ± 24	97 ± 30	84 ± 15	111 ± 29	44 ± 17
	N + P	0.012↑	82 ± 23	112 ± 33	241 ± 81	241 ± 70	157 ± 41
	P		103 ± 15	103 ± 16	80 ± 26	85 ± 25	70 ± 26
	Control		123 ± 28	114 ± 21	100 ± 23	124 ± 12	99 ± 14
Luzula spicata	Ca		21 ± 8	20 ± 7	17 ± 6	24 ± 11	17 ± 14
	H_2O		13 ± 4	18 ± 7	6 ± 4	7 ± 3	92 ± 91
	N		23 ± 11	19 ± 11	19 ± 9	21 ± 10	10 ± 7
	N + P	0.002↑	20 ± 12	33 ± 15	63 ± 36	125 ± 44	104 ± 51
	P		13 ± 5	14 ± 5	1 ± 1	12 ± 5	5 ± 2
	Control		8 ± 8	1 ± 1	3 ± 1	3 ± 1	0 ± 0
Trifolium polyphyllum	Ca		192 ± 78	194 ± 157	256 ± 131	284 ± 152	268 ± 121
	H_2O		82 ± 44	76 ± 52	94 ± 49	87 ± 44	79 ± 39
	N	ns↑	163 ± 94	190 ± 110	337 ± 195	293 ± 171	425 ± 246
	N + P		111 ± 91	112 ± 90	149 ± 130	101 ± 82	141 ± 126
	P		153 ± 88	156 ± 100	213 ± 141	223 ± 147	216 ± 138
	Control		110 ± 63	117 ± 67	212 ± 161	125 ± 79	124 ± 74

APPENDIX 3

Annual changes in numbers of generative shoots induced by experimental treatments over the period 1999–2002; 1998 values are used as a control. Mean values of number of generative shoots per square meter and their standard errors ($n = 4$) are shown. Data are presented for all the species that showed a significant or a large-magnitude (although statistically not significant [ns]) response to at least one of the treatments. Arrows ↑ and ↓ indicate increase and decrease, respectively. *P* level indicates the significance of difference between mean values of generative shoots at each respective treatment and control analyzed via repeated-measures ANCOVA with planned contrasts.

Plant	Treatment	*P* level	1998	1999	2000	2001	2002
Alchemilla caucasica	Ca		7.3 ± 4.4	2.0 ± 1.6	5.3 ± 2.4	4.7 ± 3.2	6.7 ± 2.9
	H_2O		0.0 ± 0.0	0.4 ± 0.4	2.0 ± 1.2	0.7 ± 0.4	1.1 ± 0.7
	N		0.7 ± 0.7	0.4 ± 0.4	4.0 ± 2.4	2.4 ± 1.2	1.3 ± 1.3
	N + P	0.033↑	4.4 ± 2.3	2.0 ± 1.2	18.0 ± 9.2	11.1 ± 4.1	17.1 ± 6.3
	P		9.1 ± 3.2	4.4 ± 2.1	10.7 ± 4.0	5.1 ± 1.7	5.3 ± 1.1
	Control		7.3 ± 2.9	2.0 ± 0.8	4.4 ± 1.3	5.7 ± 2.9	7.3 ± 3.3
Carex spp	Ca		0.4 ± 0.4	0.4 ± 0.4	3.3 ± 1.7	0.0 ± 0.0	7.3 ± 2.4
	H_2O		3.1 ± 1.3	3.1 ± 1.2	4.0 ± 1.5	1.1 ± 1.1	3.7 ± 1.7
	N	0.009↑	5.7 ± 2.3	1.7 ± 0.7	21.7 ± 5.2	23.7 ± 20.3	34.7 ± 17.1
	N + P	<0.001↑	3.1 ± 1.7	3.7 ± 1.2	28.0 ± 9.2	22.4 ± 11.7	38.7 ± 8.7
	P		4.4 ± 1.2	5.1 ± 3.1	4.7 ± 2.0	0.4 ± 0.4	6.4 ± 3.1
	Control		2.4 ± 1.6	0.7 ± 0.4	3.3 ± 1.6	0.0 ± 0.0	4.0 ± 2.1
Festuca ovina	Ca		33.7 ± 12.3	1.3 ± 0.9	55.7 ± 26.0	21.3 ± 4.0	37.7 ± 2.3
	H_2O		41.1 ± 6.0	3.3 ± 2.0	71.7 ± 14.9	28.7 ± 6.5	28.7 ± 8.7
	N		34.4 ± 6.1	0.4 ± 0.4	44.0 ± 5.7	11.1 ± 6.1	12.0 ± 0.9
	N + P	<0.001↑	38.0 ± 8.4	2.7 ± 1.5	558.4 ± 82.1	182.0 ± 27.3	313.7 ± 41.9
	P	<0.001↑	42.7 ± 5.5	8.0 ± 5.6	116.4 ± 22.5	87.7 ± 16.1	155.3 ± 32.7
	Control		46.4 ± 19.3	2.4 ± 1.1	68.7 ± 21.7	24.4 ± 7.7	32.4 ± 9.6
Helictotrichon versicolor	Ca		9.3 ± 4.0	0.0 ± 0.0	2.4 ± 1.1	0.0 ± 0.0	2.4 ± 1.9
	H_2O		4.0 ± 1.1	0.0 ± 0.0	4.4 ± 2.3	0.0 ± 0.0	0.7 ± 0.7
	N		5.7 ± 2.1	0.0 ± 0.0	16.7 ± 4.1	0.4 ± 0.4	2.0 ± 0.8
	N + P	<0.001↑	5.1 ± 1.5	0.0 ± 0.0	79.3 ± 16.7	15.3 ± 2.4	31.1 ± 10.4
	P		7.1 ± 0.8	0.0 ± 0.0	11.1 ± 1.5	0.0 ± 0.0	2.0 ± 0.8
	Control		3.3 ± 1.3	0.0 ± 0.0	3.3 ± 1.7	0.4 ± 0.4	0.7 ± 0.4
Luzula spicata	Ca		1.3 ± 0.9	0.0 ± 0.0	0.4 ± 0.4	0.0 ± 0.0	0.4 ± 0.4
	H_2O		2.4 ± 0.8	1.1 ± 0.7	0.4 ± 0.4	0.0 ± 0.0	0.7 ± 0.7
	N		3.1 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.4	1.1 ± 0.7
	N + P	<0.001↑	3.3 ± 1.3	1.1 ± 1.1	9.7 ± 3.2	5.7 ± 2.5	13.3 ± 5.9
	P		1.1 ± 0.7	0.7 ± 0.7	2.0 ± 1.2	0.4 ± 0.4	2.0 ± 1.6
	Control		2.7 ± 1.1	0.7 ± 0.7	1.7 ± 1.2	0.4 ± 0.4	0.4 ± 0.4
Ranunculus oreophilus	Ca		1.1 ± 1.1	1.1 ± 0.7	1.1 ± 1.1	0.7 ± 0.7	6.0 ± 2.4
	H_2O		0.0 ± 0.0	1.3 ± 0.5	0.7 ± 0.7	2.0 ± 0.8	5.7 ± 1.3
	N		0.4 ± 0.4	0.0 ± 0.0	1.1 ± 1.1	1.1 ± 0.7	4.4 ± 2.7
	N + P	0.016↑	0.4 ± 0.4	2.7 ± 1.2	3.3 ± 1.3	2.0 ± 0.7	10.0 ± 4.0
	P	0.023↑	1.1 ± 0.7	4.7 ± 0.8	4.0 ± 1.2	2.4 ± 1.2	7.1 ± 1.5
	Control		0.4 ± 0.4	2.0 ± 1.3	0.7 ± 0.4	0.0 ± 0.0	2.7 ± 1.2
Trifolium polyphyllum	Ca		0.7 ± 0.7	0.4 ± 0.4	1.3 ± 0.9	0.4 ± 0.4	0.7 ± 0.7
	H_2O		3.7 ± 1.9	5.3 ± 4.0	6.7 ± 3.3	4.0 ± 3.6	7.1 ± 4.4
	N	ns↑	0.0 ± 0.0	1.3 ± 1.3	14.4 ± 10.7	10.4 ± 6.1	31.3 ± 19.6
	N + P		0.0 ± 0.0	0.7 ± 0.7	1.1 ± 0.7	2.0 ± 0.8	1.3 ± 0.9
	P		1.7 ± 0.7	2.0 ± 1.2	3.7 ± 1.7	1.7 ± 1.7	1.7 ± 1.1
	Control		1.1 ± 0.7	0.7 ± 0.4	2.4 ± 1.6	0.0 ± 0.0	2.7 ± 0.8
Veronica gentianoides	Ca		0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.4
	H_2O		0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.4	0.4 ± 0.4	1.1 ± 0.7
	N		0.7 ± 0.4	0.0 ± 0.0	1.7 ± 1.2	0.0 ± 0.0	0.4 ± 0.4
	N + P	0.025↑	0.0 ± 0.0	0.0 ± 0.0	2.4 ± 1.1	1.1 ± 0.7	3.3 ± 1.2
	P		0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	2.4 ± 2.4	1.1 ± 0.7
	Control		0.4 ± 0.4	0.4 ± 0.4	0.0 ± 0.0	0.4 ± 0.4	1.3 ± 0.8