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Influence of soil nutrient availability on generative production in an alpine heath, the North-Western Caucasus

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Abstract. An alpine lichen heath response to changes in the soil nutrient and water availability was examined, focused on changes in generative production (number of generative shoots and seed production). A four-year experiment was conducted at a lichen heath at approximately 2,800 meters above sea level. The experimental treatment consisted of Ca, P, N, NP amendments and irrigation.

The experiment indicated that the generative production of alpine heath plants was strongly affected by nutrient availability. All graminoids analyzed in the experiment (*Festuca ovina*, *Helictotrichon versicolor, Luzula spicata* and sedges) showed a strong positive response to the NP-treatment. *Alchemilla caucasica* and *Ranunculus oreophilus* were positively affected by the NP treatment, *Trifolium polyphyllum* and *Anemone speciosa* by the N treatment and *Antennaria dioica* by the P treatment. Irrigation did not have any effect on generative shoot abundance, except for *Euphrasia ossica*, which showed a strong increase.

Fertilization had significant effects on seed production, which however did not directly correlate with changes in abundance of generative shoots. NP treatment increased seed production of *Festuca ovina* and decreased seed production of *Campanula tridentata*. Irrigation, P and Ca treatments lead to an increase in seed production of *Anemone speciosa*. Seed production of *Carum caucasicum* decreased in response to all the treatments.

Key words: alpine heath, fertilization, irrigation, resource limitation, generative, seed production

Introduction

It is commonly agreed that resource availability strongly affects the structure and dynamics of plant communities (MacArthur 1984; Tilman 1982; Tilman 1988; Rabotnov 1985). Some studies investigate how individual species are affected by changes in nutrient availability (Totland 1997; Dyer and Rice 1999). Such research demonstrates that species differ in their ability to react to changes in soil nutrient level. Thus, the patterns of reactions to change of nutrient availability, on the level of individual species as well as on a community level, still give challenging questions for research. It is presumed that alpine plants are limited mainly by nitrogen (Körner 1999). Therefore the role of other nutrients and water is often neglected by researchers and remains unknown.

Tilman (1982) showed that plant communities growing on poor-nutrient soils are more strongly affected by changes in nutrients availability then those growing on rich soils. Alpine lichen heath occurs on nutrient-poor soils. Fertilization therefore would have there a big impact on primary production. However patterns of influence of soil nutrient availability on alpine heath plants remain largely unexplored.

There have already been investigations on the reaction of grassland plant communities to changes in resource availability. Most of them however concern lowland grasslands (Huber 1994; Braakhekke and Hooftman 1999; Tilman 1982) or old fields (Wilson and Tilman 1991; Dyer and Rice 1999). There have been only a few attempts to investigate such a question in alpine tundra communities (Bowman 1994; Däler 1992). Relatively more attention was given to the constraints of nutrient availability in arctic tundra (Jonasson 1992; Shaver and Chapin 1995). The alpine tundra differs from the arctic tundra in patterns of soil moisture, light regimes etc (Billings 1974). Although some climatic issues of the arctic tundra seem to be similar to the alpine tundra, the direct transfer of the knowledge obtained in the studies of arctic tundra onto plant communities of alpine tundra is not possible.

The objective of our study was to examine the response of an alpine heath plant community to changes in the soil nutrient and water availability induced by fertilization and irrigation. We were interested in relative abundance among the species of one community and in the influence of difference resources on these patterns.

Previous investigations on the same site showed that through absents of clonal propagation, 42 % of species reproduce only by seeds. 55 % of species use both seed and vegetative reproduction. (Grishina *et al.* 1986). In spite of importance of generative reproduction, little is known about influence of soil fertility on flowering and seed production on alpine heath. In this research we therefore focussed on the tendencies of changes in number of generative shoots and seed production in responds to increase of soil nutrient availability.

We addressed the following three questions: (1) How does the number of generative shoots of various species change under fertilization treatments? (2) How is seed production of various species influenced by soil nutrient availability? (3) How is biodiversity and species richness in terms of generative shoots influenced by fertilization?

To answer these questions a four-year experiment was conducted at a lichen heath at approximately 2,800 meters above sea level. The experimental treatment consisted of Ca, P, N, NP amendments and irrigation. In this article we discuss the changes that occurred after three years of nutrient supplement.

Material and Methods

Study site

The research was conducted at the Teberda Biosphere Reserve (the Northwestern Caucasus, Russia). The experimental site is located in an alpine lichen heath on the south windward slope of the Mt. Malaya Khatipara (43˚27'N, 41˚42'E at approximately 2,800 meters above sea level). The climate is characterized by low air temperatures (mean annual temperature is –1.2˚C, mean July temperature is 7.9˚C) and high wind velocities. Although annual precipitation in the region is high (1,400 mm), the majority falls in the winter as snow. Due to the position on a windward slope most of the snow is blown away from the site. The vegetative season lasts 5 months from May till September. Details about the site location and climate can be found in Grishina *et al.* (1986), Onipchenko and Blinnikov (1994).

Fruticose lichens (mainly *Cetraria islandica*) are the main dominant of the site. Of the vascular plants most common are *Anemone speciosa, Antennaria dioica, Trifolium polyphyllum, Festuca ovina, Carex sempervirens, Carex umbrosa*. Plant cover consists of patches of vascular plants alternating with lichen areas. Lichen cover about 50-60% of the area. The typical size of lichen and vascular plant patches is about 5-10 cm across (Onipchenko and Blinnikov 1994).

More detailed descriptions of the site plant community can be found in Onipchenko (1994).

Experimental design

The experiment took place in the 4 year period from 1998 till 2001. During this period climate conditions varied strongly. The year of 1998 was very dry. During the period from April till October the precipitation monthly level was constantly 1.5-20 times lower then average. The year of 2000 was also rather dry (especially July when the precipitation level was 7 times lower then average). During the years of 1999 and 2001 the precipitation level did not differ strongly from the average.

The experiment was carried on in 6 variants (control, P, N, NP, Ca and irrigation). A uniform area of 19x6.5 m was selected on the site and divided into 24 1.5x1.5 m plots separated from each other by a 1 m buffer zone. The plots were randomly assigned as control, P fertilized, N fertilized, NP fertilized, Ca fertilized and irrigated plots (further referred to as H_2O plots). Each plot contained three subplots of 0.5x0.5 m situated at the top of the plot. The bottom part of the plot contained subplots where the number of vegetative shoots was analyzed. This analysis is the subject of a separate article. The experimental design is presented in Figure 1.

During the first experimental year (1998) no treatment was applied to the plots but sampling was performed. The data about the initial plant abundance on the subplots was thus obtained. In 1999 Ca, N, P and NP fertilization was applied. Next years the N, P and NP plots were fertilized once per year in May. In the years 1999-2001 the H_2O plots were irrigated during the vegetation period (from middle June till August).

The fertilization was conducted as follows:

* On Ca plots lime (52 g.m^{-2} of ($Ca(OH)_2$) was used as a source of Ca once in 1999 year;
* On N plots urea was used as a source of N (9 g. m^{-2} yr^{-1});
* On P plots double superphosphate was used as source of P (6 g.m^{-2} yr^{-1} of P_2O_5);
* On NP plots urea and double superphosphate were used as source of N and P (9 and 6 g.m^{-2} yr^{-1} respectively).

The H_2O plots were irrigated applying enough water to compensate the evapotranspiration of the stand. The daily value of evapotranspiration is (3.2 mm) (Grishina *et al.* 1986). Every day the precipitation was measured. If the precipitation over the 3-day period did not compensate the water loss due to evapotranspiration, irrigation was done.

Field observations

The plots were examined once per year in the end of July at the middle of the growth season. In each subplot we counted the number of flowering shoots per species. This was done for all species that occur on the subplots. The selection of species for further study was based on the number and frequency of species shoots.

The following species were chosen for the study: *Alchemilla caucasica* Buser, *Anemone speciosa* Adams ex G.Pritz., *Antennaria dioica* (L.) Gaertn., *Arenaria lychnidea* Bieb., *Campanula collina* Bieb., *Campanula tridentata* Schreb., *Carex sempervirens* Vill., *Carex umbrosa* Host, *Carum caucasicum* (Bieb.) Boiss., *Erigeron alpinus* L., *Euphrasia ossica* Juz., *Festuca ovina* L., *Fritillaria collina* Mill, *Gentiana pyrenaica* L., *Gentiana verna* L., *Helictotrichon versicolor (Vill.)* Pilger, *Luzula spicata* (L.) DC., *Minuartia circassica* (Albov) Woronow, *Oxytropis kubanensis* Leskov, *Pedicularis caucasica* Bieb., *Plantago atrata* Hoppe, *Potentilla gelida* C.A.Mey., *Polygonum bistorta* L. *Primula algida* Adams., *Ranunculus oreophilus* Bieb., *Trifolium polyphyllum* C.A.Mey., *Veronica gentianoides* Vahl.

Data analysis

The influence of fertilization and irrigation on the number of flowering shoots was analyzed using Repeated Measures ANOVA. In the analysis the

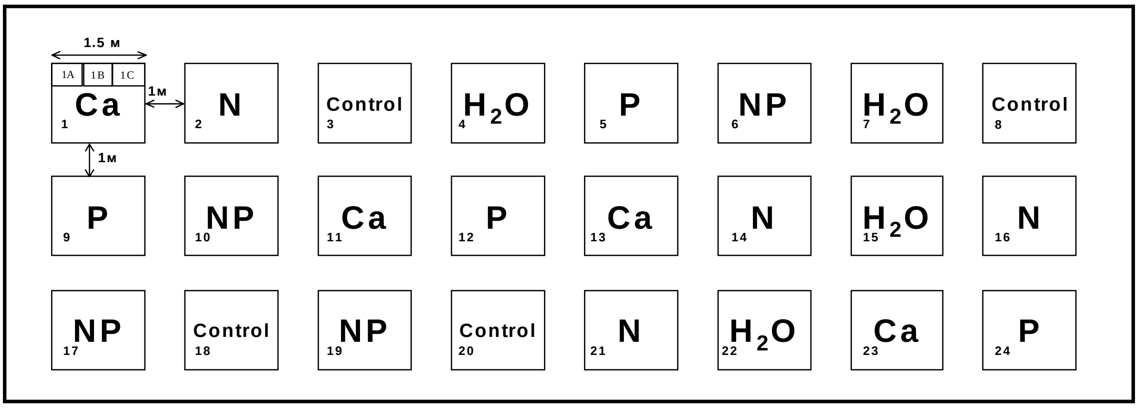

Fig. 1. Experimental design.

treatments were considered as between-subject variables (fixed factors). Transformed data of flowering shoots per subplot observed in 1999-2001 was considered as within-subject variables. The transformation implying the standardization of data was performed for every species as follows:

Step 1: The total sum of generative shoots observed in 1998 (the first year of the experiment, when no fertilizer was added) was calculated for every treatment.

Step 2: The data of the shoot numbers observed in the next years per plot were divided by the initial sum for the respective treatment.

This transformation enabled us to compensate the influence of initial shoot number on the analyses. For *Trifolium polyphyllum* in N and NP variants no shoots were observed in 1998. Later however we observed a strong increase of the shoot number in N variant (see Table 2). In this case step 2 of the transformation would require dividing by zero. We considered the total sum of shoots calculated in step 1 to be equal 1. Then in step 2 the shoot numbers observed in the following years were divided by 1.

The influence of experimental treatments on the biodiversity was estimated via analysis of species richness and the Shannon-Wiener index. The species richness was measured as a number of flowering species observed per subplot. Both measures were analyzed using Repeated Measures ANOVA.

The seed production of four species (*Anemone speciosa*, *Campanula tridentata*, *Carum caucasicum* and *Festuca ovina*) was analyzed based on the data of the last experimental year (2001). 10 or less (if 10 were not available) generative shoots per plot were collected just before ripping. The number of well-developed seeds was counted. For each species an ANOVA analysis was performed.

When a significant ANOVA result occurred, Tukey's honestly significant difference test and the least significant level test (LSD test) were used to determine differences among means. Tukey's test is known to be stricter than the LSD test. Therefore we considered results that were confirmed by Tukey's test to be more reliable than those confirmed only by the LSD test. In the latter case an additional analysis taking into consideration the actual abundance of the shoots (the not standardized value of the shoots number) and the distribution of the shoots through the subplots was always performed. The critical significance level was $P < 0.05$ for all analyses.

Results

Graminoids

All graminoids analyzed within the experiment (*Festuca ovina*, *Helictotrichon versicolor*, *Carex sepervirens*, *Carex umbrosa*, *Luzula spicata*) were affected by the NP-treatment. The number of flowering shoots increased sharply. The number of flowering shoots for all the species was however higher in the year 2000 (the third year of the experiment) than in the year 2001 (the fourth year of the experiment). This was possibly due to a very dry summer in 2000. Another possible reason for this effect is the increase of the biomass of the plants caused by fertilization, which resulted in the relative decrease of the shoot number, while shoots became noticeably bigger. Nevertheless the number of shoots occurring in 2001on NP-treated plots was significantly higher then the number of shoots on other plots. Other treatments did not cause a significant response within graminoids. The absolute (not standardized) values of total sums of shoots per treatment are presented in Table 1. Figure 2 demonstrates the changes of mean value of standardized numbers of shoots per treatment.

In NP variant the magnitude of increase for *Festuca ovina* and *Helictotrichon versicolor* was 1,500% in 2000 and 300-500% in 2001, respectively. Sedges *(Carex sempervirens and Carex umbrosa)* were analyzed as one group. They were less influenced by the dry summer of 2000. In the NP variant the increase in the years 2000 and 2001 was 930% and 740% respectively. *Luzula spicata* showed the smallest reaction to NP treatment of all the graminoids. The increase was around 290% in 2000 and 170% in 2001. A LSD test detected the effect of P-treatment to be significant compared to Ca, H_20 and N treatments, but this was not confirmed by Tukey's test, probably due to the small number of the shoots (see Table 1).

Forbs

In contrast to the graminoids, which only showed a significant response to the NP treatment, species of other life forms also showed a response to other treatments. The absolute values of the total sum of shoots per treatment and their mean values are summarized in Table 2. Figure 3 demonstrates the changes of mean value of the standardized numbers of shoots per treatment.

Irrigation increased the number of shoots of *Euphrasia ossica* significantly in the last experimental year (2001). The number of shoots rose 3,000% in comparison with the year 1998. The number of shoots varied strongly depending on the dry and wet summers. Table 2 shows that in 1999, as a result of a dry summer in 1998 (when no irrigation was conducted), no shoots were observed on any plot. In 2000 the number of shoots was still not high, probably due to small amount of seeds produced in 1999. Only in 2001 after three years of irrigation was there a significant increase of shoots on the irrigated plots, in comparison to the number of shoots counted on the other plots.

Alchemilla caucasica showed an increase of approximately 500% in response to the NP treatment. The LSD test gave a positive result for comparison of both the N and NP treatments with the controls. The Tukey's test however did not confirm these results. Taking into account the actual number of annually observed shoots (1-12 on N fertilized plots and 6-84 on NP fertilized plots, see Table 2), we consider only the increase for the NP treatment to be a significant result (despite the positive LSD test for N-treatment and the obvious tendency of growth on the graph in Figure 3).

Ranunculus oreophilus, was also affected by the NP treatment. The LSD test detected a significant difference in the number of shoots on NP treated plots from controls and plots with other treatment. The Tukey's test showed a significant difference only in the comparison of the N treatment with the Ca treatment.

Trifolium polyphyllum was strongly affected by N treatment. The number of flowering shoots changed from zero in 1998 to 43 and 31 in 2000 and 2001 respectively. It is interesting to note that the NP treatment did not cause a significant change in the number of shoots. This was possibly due to a stronger competition with graminoids on NP plots.

Anemone speciosa showed a positive response to the N treatment. However on control plots we also observed a rise in shoot numbers (although the increase was smaller). Because of this there was no consistent difference between the N treated plot and the control plots. The LSD test however detected a difference between the N treatment and some other treatments, namely Ca, H_2O and P treatments. This result was not confirmed by the Tukey's test.

Antennaria dioica was affected by P treatment. However due to the strong variability through the years and insufficient total number of shoots (see Table 2) we consider this result to require more years of observations to be confirmed.

Seed production

Seed production of all the studied plants was affected by treatments. The effects of fertilization and irrigation however differed strongly between plants. The mean values of seed number per shoot are presented in Figure 4.

Anemone speciosa tended to increase seed production in response to the P treatment (260%), Ca treatment (350%), and irrigation (230%) in comparison with the control (See Figure 4). These results however were not statistically significant.

Species	Variant	1998	1999	2000	2001
Carex spp.	Ca	1	1	10	0
	Control	7	2	10	0
	H_20	9	9	12	3
	N	17	5	65	71
	NP	9	11	84	67
	P	13	15	14	1
Festuca ovina	Ca	101	4	167	64
	Control	139	7	206	73
	H_20	123	10	215	86
	N	103	1	132	33
	NP	114	8	1,675	546
	P	128	24	349	263
Helictotrichon versicolor	Ca	28	0	7	0
	Control	10	0	10	1
	H20	12	0	13	0
	N	17	0	50	1
	NP	15	0	238	46
	P	21	0	33	0
Luzula spicata	Ca	4	0	1	0
	Control	8	2	5	1
	H20	7	3	1	0
	N	9	0	0	1
	NP	10	3	29	17
	P	3	2	6	1

Table 1. Graminoids. The absolute (not standardized) values of total sums of shoots per treatment.

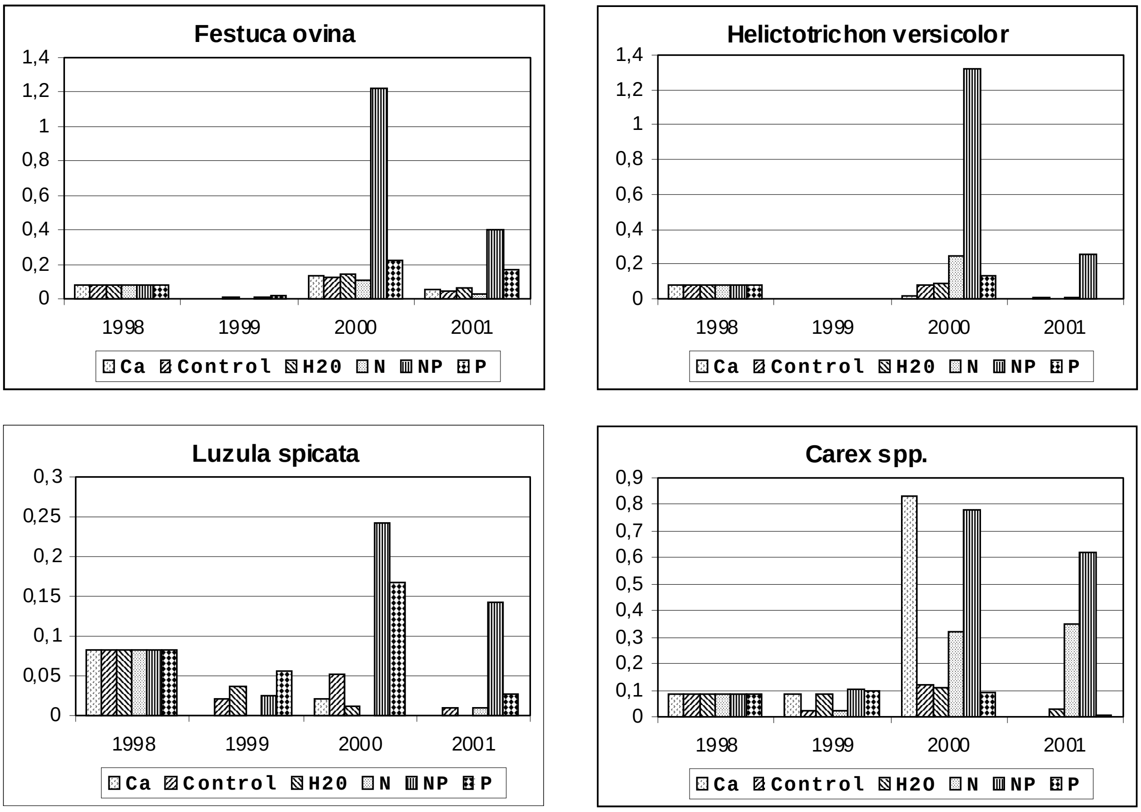

Fig. 2. Changes of mean of standardized shoot numbers per treatment for graminoids.

The reaction of *Campanula tridentata* differed for different treatments. The NP fertilization caused a significant decrease in seed production (260%). We observed tendencies to decrease under N treatment and to increase under P treatment, but those were not statistically significant.

The seed production of *Carum caucasicum* decreased with all the treatments in comparison with control. The significant decrease was detected only by LSD test and was not confirmed by Tukey's test. The decrease amounted to 200% for N treatment, 190% for Ca treatment and 230% for irrigation.

Festuca ovina showed a significant response only to NP treatment. The seed production increased 190%.

Biodiversity

Analyzes of the biodiversity showed that so far no single treatment caused any significant changes in the value of Shannon-Wiener index. The species richness (the number of species with generative shoots) increased in response to the NP treatment. The increase was about 150%. The other treatments did not affect the biodiversity.

Discussion

Changes in generative shoots

The experiment indicated that the generative production of alpine heath plants is strongly affected by nutrient availability. Dominants as well as non-dominant species were affected by treatments. All the species showed however strong annual variability caused by weather conditions.

Several studies prove that N and P are the most limiting nutrients in respect of plant size as well as shoot numbers (Bowman 1994; Berendse and Outdorf 1998; Harrison *et al.* 1994; Heil and Diemont 1983; Stevens and Carson 1999; Shaver and Chapin 1995; Wilson and Tilman 1991). Our results support this suggestions. Our experiments indicate that graminoids are strongly limited by both N and P elements when other forbs can be only N or only P deficient.

We found that species richness in respect to flowering plants increased in response to the NP treatment, but the variability characterized by the value of Shannon-Wiener index did not show any significant changes. Stevens and Carson (1999) also reported increase of species richness as a result of supply of small amounts of NP fertilizer. Their research was aimed at analysis of the change of a plant community along the soil fertility gradient. In contract to our research, which is aimed on analysis generative shoot number, their analysis was based on the vegetative production.

All the graminoids showed a strong increase in response to NP treatments. This is consistent with the results of Wilson and Tilman (1991) and Jonasson (1992) that were obtained in the similar experiments. These researches were however based on analysis of a vegetative production (measured as dry weight of standing crop and vertically projected plant area respectivly). None of our target graminoid species were affected by amendment of N only. This result suggests that flowering of graminoids on alpine heath is limited by both N and P elements.

In contradiction to generative shoots of graminoids, generative shoots of forbs were affected by various treatments. *Euphrasia ossica* showed a strong increase in response to irrigation. *Alchemilla caucasica* and *Ranunculus oreophilus*, were affected by the NP

Species	Variant	1998	1999	2000	2001
Alchemilla caucasica	Ca	22	6	16	20
	Control	22	6	13	24
	$H_2$0	0	1	6	2
	N	2	1	12	9
	NP	13	6	84	58
	P	27	13	33	22
Anemone speciosa	Ca	17	9	20	15
	Control	9	6	12	18
	$H_2$0	9	6	8	13
	N	6	4	15	18
	NP	14	7	25	20
	P	17	12	22	16
Antennaria dioica	Ca	8	1	4	6
	Control	14	0	7	6
	$H_2$0	2	10	1	7
	N	17	5	15	6
	NP	8	4	20	1
	P	1	1	6	8
Euphrasia ossica	Ca	34	0	19	72
	Control	22	0	1	73
	$H_2$0	16	0	0	487
	N	17	0	30	29
	NP	20	0	93	120
	P	18	0	11	29
Ranunculus oreophilus	Ca	3	3	3	2
	Control	1	6	2	0
	$H_2$0	0	4	2	6
	N	1	0	3	3
	NP	1	8	11	6
	P	3	14	12	7
Trifolium polyphyllum	Ca	2	1	4	1
	Control	3	2	7	0
	$H_2$0	11	16	20	12
	N	0	4	43	31
	NP	0	2	3	6
	P	5	6	11	5

Table 2. Forbs. The absolute (not standardized) values of the total sums of shoots per treatment.

treatment. *Trifolium polyphyllum* and *Anemone speciosa* showed a positive response to the N treatment. *Antennaria dioica* was affected by P treatment.

In our experiment we found that irrigation had almost no effect on the generative production. None of the perennials showed any response to withdrawal of water shortage. This result contradicts with observations made in identical series of experiments on alpine *Hedysarum-Geranium* meadow performed on a neighboring site (Cherednichenko, personal communication) where the irrigation had a major effect on generative shoots number. In our experiment the only species affected by irrigation was *Euphrasia ossi*ca. In contrast to alpine perennials annual *Euphrasia ossi*ca has tiny and relatively short roots. Although it is a hemi-parasitic species, on early stages it obtains water and nutrients from soil and depends on soil humidity. Because of this, it is probably strongly affected by droughts. Withdrawal of water shortage therefore caused a strong increase in shoot number.

The number of flowering shoots of *Trifolium polyphyllum* increased significantly with N fertilization. This is unusual for species of *Fabaceae* family, which are usually not limited by soil nitrogen due to their nitrogen fixation activity (Sprent and Sprent 1990). However a previous study at the same site (Onipchenko *et al.* 2001) showed that in contrast to other alpine species of *Trifolium* (Gigon 1999; Thomas and Bowman 1998) *Trifolium polyphyllum* does not fix nitrogen. The significant increase of *Trifolium polyphyllum* in response to N treatment gives another proof of this fact.

Seed production

Although the generative production was affected by nutrient availability, changes in seed production and number of generative shoots did not correlate directly. Only *Festuca ovina* showed both seed production and generative shoots increase in response to the same treatment (NP). The generative shoot numbers of *Carum caucasicum* and *Campanula tridentata* were not affected by treatments but their seed production decreased. A number of generative shoots of *Anemone speciosa* showed a positive response to N fertilization while the seed production increased under P, Ca and H_2O treatments.

According to Tilman's resource-ratio hypothesis competition for other resources succeeds the competition for nutrients when the nutrient availability increases. Seed production depends on nutrient availability as well as on pollination. Under NP treatment graminoids strongly increased in size and density. Therefore small plants such as *Campanula tridentata* became less accessible for insects. This probably explains the decrease of seed production of *Campanula tridentata* under NP treatment. Other forbs (*Festuca ovina, Carum caucasicum* and *Anemone speciosa*) did not have this problem, because their flowing shoots were above the canopy. Similar results were reported by Willems (2002) who analyzed how seed production of *Orchis simia* Lamk. depends on mowing.

Seed production of *Festuca ovina* strongly increased under NP treatment. It was not affected by N or P treatment. This result proves that seed reproduction of *Festuca ovina* in limited by both N and P.

Seed production of *Carum caucasicum* was affected negatively by all the treatments except NP. Seed production of *Anemone speciosa* was higher than the control on P, Ca and H_2O treated plots, but did not differ from the control on N and NP treatet plots. These results suggest that individual species vary in their needs in respect to seed production. Further study over several years is needed to detect clear patterns of these reactions.

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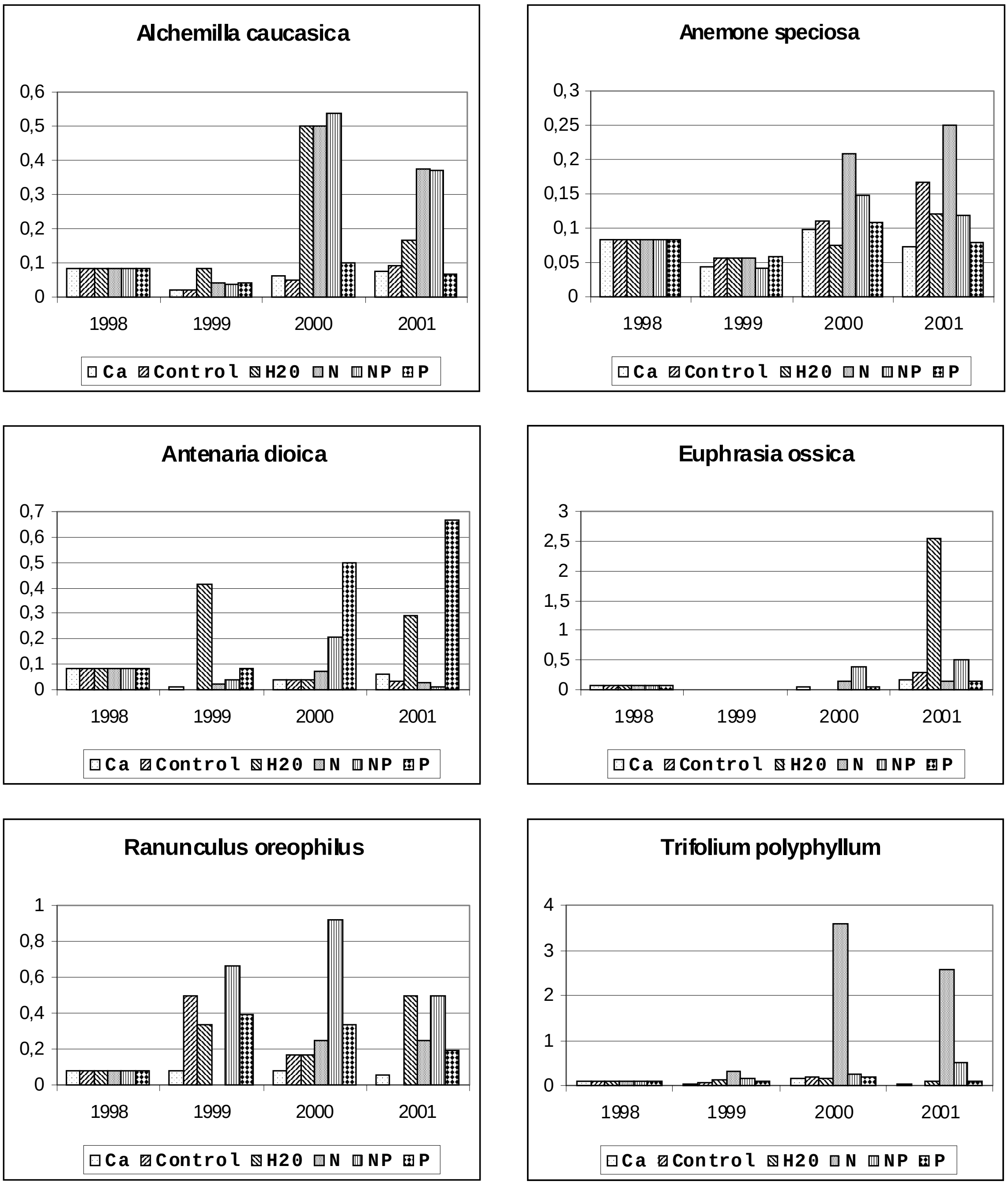

Fig. 3. Changes of mean of the standardized shoot numbers per treatment for non-graminoids.

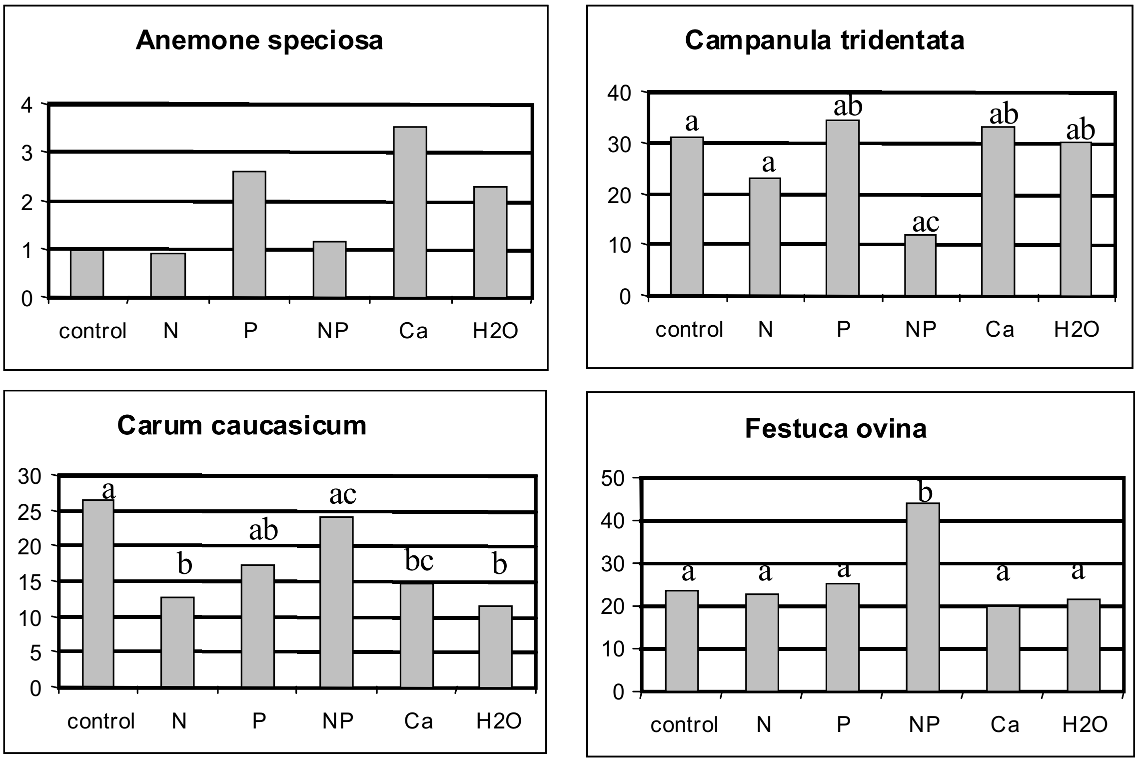

Fig. 4. Seed production. Mean values of seed number per plant. The values with the same letters have no significant difference.

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