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7. Shading experiments in alpine grasslands

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7.1. INTRODUCTION

Despite high insolation of alpine habitats, light is considered a limiting resource for plant development (KOERNER 1982). Many authors maintain that many high mountain communities consist of species with different photosynthetic attributes (ABDALADZE 1987, NAKHUTSRISHVILI 1974, 1988). Such differences may be responsible for the divergence of ecological niches and sustainment of the biological diversity of ecosystems.

The aim of this study was to investigate the influence of artificial shading on the composition and structure of *Festuca varia* dominated grasslands (FVG). This type of community is wide-spread throughout the Caucasus (GROSSHEIM 1948). The investigated community is described in chapter 1.4 of this volume. The following goals were persued: 1) determine if a temporal separation is taking place among different species; 2) reveal species most sensitive or tolerant to severe shading; 3) compare response to shading of FVGs with that of the previously studied alpine lichen heaths.

7.2. METHODS

Mainly the same methods were used as in the shading experiments in ALH (RABOTNOVA et al. 1992).

The experiment was conducted in the field in four variants: 1) control; 2) shading for the first half of the vegetative season (June-mid July); 3) shading for the second half (mid July- August); 4) shading for most of the vegetative season ("all-summer" variant, i.e., June, July, and August).

One square meter plots were shaded in triple replicability with four counting plots of a smaller size (0.25x0.25 m) in the centre, minimizing side effects. Therefore, results of each experimental variant were obtained from twelve plots.

The number of vegetative and generative shoots were counted of all vascular plant species found on the field plots fenced in by pegs and fishing line. This parameter proved to be the best indicator of a species role in the community. The number of shoots were counted in 1988 (initial year), 1989, 1990, and 1991.
For shading, two-layer cloth tents (white above and black beneath). The tents cut out about 95% of the light, providing extreme shade. The level of luminosity is close to the compensation point of many alpine plants (RABOTNOVA et al. 1992). The tents were well permeable for water and air and set at the height of 10 cm above the soil surface. Strong winds, common at high elevations, provided sufficient movement of air under the tents, so microclimatic differences between the shaded area and the rest of the community were negligible. Even under bright summer sunlight the soil surface temperature under the tents exceeded that of open places no more than 3°C.
The structure of *Festuca varia* dominated alpine grassland (FVG) fluctuates significantly from year to year. In one year some species tend to produce many more shoots than in another, whereas other species fluctuate only slightly. For example, in the control variant, *Carex umbrosa* produced almost the same amount of shoots each year (from 100-137), while *Festuca ovina* increased its shoot number from 124 in 1988 to 423 in 1992. High fluctuation is especially characteristic of the generative shoot production. Thus, *Campanula biebersteiniana* lacked generative shoots in the control in 1988 and in 1992, but produced 18 shoots in 1990.
Such fluctuations considerably complicate the interpretation of experimental data. Therefore, a relative coefficient (K) is suggested, considering both changes in number of shoots in the experiment and control.

$$K = \frac{N_{t2} \times C_{t1}}{N_{t1} \times C_{t2}}$$

N_{t1} is shoot density on the experimental plots at the beginning of the experiment, N_{t2} , shoot density on the experimental plots after a few years, C_{t1} , shoot density on the control plots at the beginning of the experiment and C_{t2} , shoot density on the control plots after the same number of years as N_{t2}. If, in a particular year, a species increases its number under experiment, but does not change in the control, than K will be more than 1. On the contrary, if the species number decreases under experiment, K will be less than 1.

On the other hand, if a species retains the same shoot quantity under experiment from year to year, but increases in control, the coefficient will be less than 1. In other words, K>1 shows that the experimental conditions were probably more favourable than those of the control, and K<1, on the contrary, shows that the experimental conditions were somewhat worse.
K was calculated for the seven, most abundant species occurring in all three experimental variants and in the control (Tab. 7.3).

7.3. RESULTS AND DISCUSSION

7.3.1. Changes on plots shaded for most of the vegetative season (all-summer variant)

Shading during most of the vegetative season significantly decreased the total number of species in the studied counting area, as well as the number of shoots produced by certain species (Tab. 7.1 and 7.2). By the third experimental year most species disappeared from the composition of the community. Total species diversity by the third year was reduced from 24 to eleven, and floristic diversity (average number of species per 0.25x0.25 m plot) from 8.5 to 1.8 (Table 7.2 and Fig. 7.1). Where at the beginning of the experiment nine species produced generative shoots, by the end not a single species attempted to flower.
Most species gradually decreased in the number of shoots during the experiment. In the second year (in 1990) five species disappeared: *Antennaria dioica, Anthemis iberica, Campanula collina, Carum caucasicum* and *Luzula multiflora*. In the following year eleven more species out of 22 disappeared. Eleven species survived till the end, but only *Anthoxanthum odoratum, Gentiana djimilensis* and *Nardus stricta* produced more than ten shoots each.
As mentioned above, the relative coefficient K was calculated for the seven, most abundant species occurring in all three experimental variants and in the control (Table 7.3). The obtained data show that in the all-summer shading (or the third) variant, six species were significantly reduced in their number of shoots, and only *Viola oreades* kept almost the same number of shoots as at the beginning. Among the rest, *Anthoxanthum odoratum* appeared to be the most stable. It confirms previous conclusions, based on shading experiments in ALHs carried out by RABOTNOVA et al. (1992), that evergreen and early developing species are more tolerant to shading because they have more time

Table 7.1. Dynamics of the number of shoots during the shading experiment in the *Festuca varia* grasslands community (FVG) in the three experimental variants and in the control. Number of generative shoots (if any) is shown after the slash (/).

Species	Number of shoots Years 88	89	90	91
Control: no shading				
Agrostis vinealis	3	2	2	2
Anemone speciosa	1	1	1 / 1	0 / 1
Antemis iberica	1	1	1	2
Antennaria dioica	99	112 / 2	118 / 1	109
Anthoxanthum odoratum	58 / 1	91 / 10	128 / 9	124 / 17
Campanula biebersteiniana	65	90 / 1	63 / 18	55
Campanula collina	5	5	2	2
Carex atrata	1	3	2	18
Carex umbrosa	91 / 9	126 / 7	135 / 2	114 / 7
Carum caucasicum	0	4	1	0
Cerastium purpurascens	0	5	0	0
Euphrasia ossica	0 / 33	0 / 28	0 / 31	0
Festuca ovina	122 / 2	269 / 9	376 / 5	394 / 29
Festuca varia	727	853 / 40	959 / 3	990 / 37
Fritillaria lutea	6	0 / 1	2	0 / 1
Galium verum	1	1	1	2
Gentiana djimilensis	1	13	15	19
Hedysarum caucasicum	1	1	1	0
Hieracium macrolepis	17 / 1	11	11	8 / 1
Hypericum polygonifolium	3	5	1	0
Nardus stricta	1285 / 21	2005 / 46	2277 / 76	2259 / 127
Ranunculus oreophilus	2	1	0	0
Scorzonera cana	3	2	4	3 / 1
Taraxacum stevenii	0	1	0	0
Veronica gentianoides	6	8	6	3
Viola oreades	96 / 1	121 / 3	87	13
Shading for the first half of the vegetative season				
Anemone speciosa	0	0	1	0
Antennaria dioica	6	6	4	0
Anthemis iberica	4	4	4	5
Anthoxanthum odoratum	54 / 2	66 / 6	78 / 2	67 / 3
Calamagrostis arundinacea	114	132	112	71
Campanula biebersteiniana	3	2	4	2
Campanula collina	6 / 1	4	1 / 1	2
Carex atrata	0	0	2	13
Carex umbrosa	65	82 / 3	80 / 2	102
Cerastium purpurascens	2	4	1	0
Deschampsia flexuosa	296 / 4	436 / 8	178	27
Erigeron venustus	18	16	14 / 1	17 / 1
Euprasia ossica	0 / 29	0 / 2	0	0
Festuca ovina	74 / 1	149 / 3	100 / 1	92 / 2
Festuca varia	760	806 / 10	562	495

Table 7.1. (continued)

Species	Number of shoots Years 88	89	90	91
Gentiana biebersteinii	0	0 / 22	0	0
Gentiana djimilensis	40 / 8	68 / 1	55 / 7	70
Gentiana septemfida	44	2	0	0
Helictotrichon versicolor	3	7	0	0
Luzula multiflora	3	1	0	0
Minuarta recurva	0	22 / 3	0	0
Nardus stricta	1075 / 11	1106	1106	1086
Plantago saxatilis	4	0	0	0
Ranunculus oreophilus	41 / 3	27 / 2	15	9 / 1
Scorzonera cana	0	2	0	0
Vaccinium vitis-idaea	2	7	4	2
Veronica gentianoides	1	2	3	0
Viola oreades	47	38	29	4
Shading for the second half of the vegetative season				
Ajuga orientalis	1	0	2	1
Antennaria dioica	25	23	12	0
Anthemis iberica	4	4	1	0
Anthoxanthum odoratum	28 / 1	30 / 4	35	18
Campanula biebersteiniana	9	4	7	4
Campanula collina	6	3	2	0
Carex atrata	4	4 / 1	4	4
Carex umbrosa	47	47 / 3	63 / 1	51
Carum caucasicum	9	8	5	1
Cerastium purpurascens	0	2	0	0
Euphrasia ossica	0 / 3	0	0 / 1	0
Festuca ovina	0	14 / 2	7	15
Festuca varia	761	1059 / 43	958 / 1	688
Fritillaria lutea	3 / 1	0	0	0
Gentiana djimilensis	45 / 1	26 / 1	19 / 1	17
Gnaphalium supinum	0	0	3	0
Helictotrichon versicolor	7	10	15	15
Leontodon hispidus	3	2	3	2
Deschampsia flexuosa	0	0	10	0
Nardus stricta	935 / 3	1203	1100	728
Ranunculus oreophilus	13	12	7	7 / 1
Scorzonera cana	1	2	3	0
Senecio aurantiacus	1	1	0	1
Taraxacum stevenii	0	0	1	0
Veronica gentianoides	5	4	3	4
Viola oreades	45	71	50	16
Shading for the whole vegetative season				
Antennaria dioica	4	10	0	0
Anthemis iberica	27	11	0	0

Table 7.1. (continued)

Species	Number of shoots Years			
	88	89	90	91
Anthoxanthum odoratum	28 / 5	29 / 3	24	11
Bromopsis variegata	0	0	2	0
Calamagrostis arundinacea	281 / 1	309 / 4	47	7
Campanula collina	2	1 / 1	0	0
Carex atrata	1	0	4	0
Carex umbrosa	81 / 2	95 / 4	37	6
Carum caucasicum	1	1	0	0
Cerastium purpurascens	15 / 2	11 / 6	20	9
Erigeron venustus	14	14	4	0
Euphrasia ossica	0 / 83	0 / 33	0 / 3	0
Festuca ovina	123 / 3	122 / 2	15	0
Festuca varia	361	279 / 8	73	2
Fritillaria lutea	2	0	3	0
Gentiana djimilensis	41	46 / 5	47 / 2	19
Gnaphalium supinum	0	0	1	0
Leontodon hispidus	11	8	10	0
Luzula multiflora	4 / 1	2 / 2	0	0
Minuartia aisoides	7	0	0	0
Nardus stricta	1288 / 35	1097 / 3	300	45
Pedicularis chroorhyncha	0	0	0	1
Ranunculus oreophilus	20 / 3	13 / 1	6	0
Scorzonera cana	0	0	1	0
Taraxacum stevenii	1	1	1	0
Vaccinium vitis-idaea	3	3	4	3
Veronica gentianoides	17	11	15	2
Viola oreades	43	47	35	5

available for photosynthesis (BORISOVA et al. 1972). *Viola oreades* is a stress-tolerant species, highly tolerant to shading, and *Anthoxanthum odoratum* is a rather tolerant, partially winter-green grass (SYDES and GRIME 1984).

Table 7.1 shows, that a few other winter-green species (particularly *Calamagrostis arundinacea, Carex umbrosa* and *Gentiana djimilensis*) also increased in the general number of shoots in the second year of experiment. *Gentiana djimilensis* even produced generative shoots throughout the experiment. Possibly, this group of species gains competition advantage because of its high shading tolerance. However, these observations do not consider the simultaneous rise in the shoot number of these species in the control plots during the same year.

Table 7.2. Amount of species and floristic richness of *Festuca varia* dominated grasslands in shading experiments.
Above line: total amount of vascular plant species found in a variant (amount of species producing generative shoots is shown in parentheses); below line: floristic diversity (number of species per plot 0.25 x 0.25 m, average and standard error).

Year	1988	1989	1990	1991
Variant control:				
no shading	23(7)	26(10)	23(9)	19(9)
	-----------	-----------	-----------	-----------
	7.8 + 1.0	8.0 + 0.9	7.8 + 1.0	6.3 + 0.8
Experiment:				
shading for	22(8)	24(10)	20(6)	17(3)
the 1st half	-----------	-----------	-----------	-----------
of the summer	8.3 + 1.2	8.6 + 1.3	7.0 + 1.0	5.3 + 0.8
shading for	21(4)	20(5)	23(4)	16(1)
the 2nd half	-----------	-----------	-----------	-----------
of the summer	5.9 + 1.1	5.7 + 0.9	6.3 + 1.0	4.2 + 0.7
shading for	24(9)	21(12)	21(2)	11(0)
the whole	-----------	-----------	-----------	-----------
summer	8.5 + 1.6	7.3 + 1.0	6.0 + 1.1	1.8 + 0.5

Table 7.3. Relative coefficient (K) in shading experiments calculated for the seven most abundant species of FVGs.

	Variant								
	1st half			2nd half			all summer		
Years	89	90	91	89	90	91	89	90	91
Species									
Anthoxanthum odoratum	0.58	0.62	0.52	0.68	0.52	0.26	0.57	0.31	0.140
Carex umbrosa	0.98	0.92	1.30	0.80	0.99	0.90	0.90	0.32	0.060
Festuca ovina	0.90	0.44	0.37	-	-	-	0.44	0.04	-
Festuca varia	0.87	0.56	0.46	2.14	0.95	0.64	0.65	0.15	0.004
Gentiana djimilensis	0.11	0.09	0.08	0.05	0.03	0.02	0.10	0.08	0.020
Nardus stricta	0.65	0.57	0.55	0.82	0.65	0.42	0.53	0.13	0.020
Viola oreades	0.63	0.69	0.64	1.23	1.24	2.65	0.86	0.91	0.870

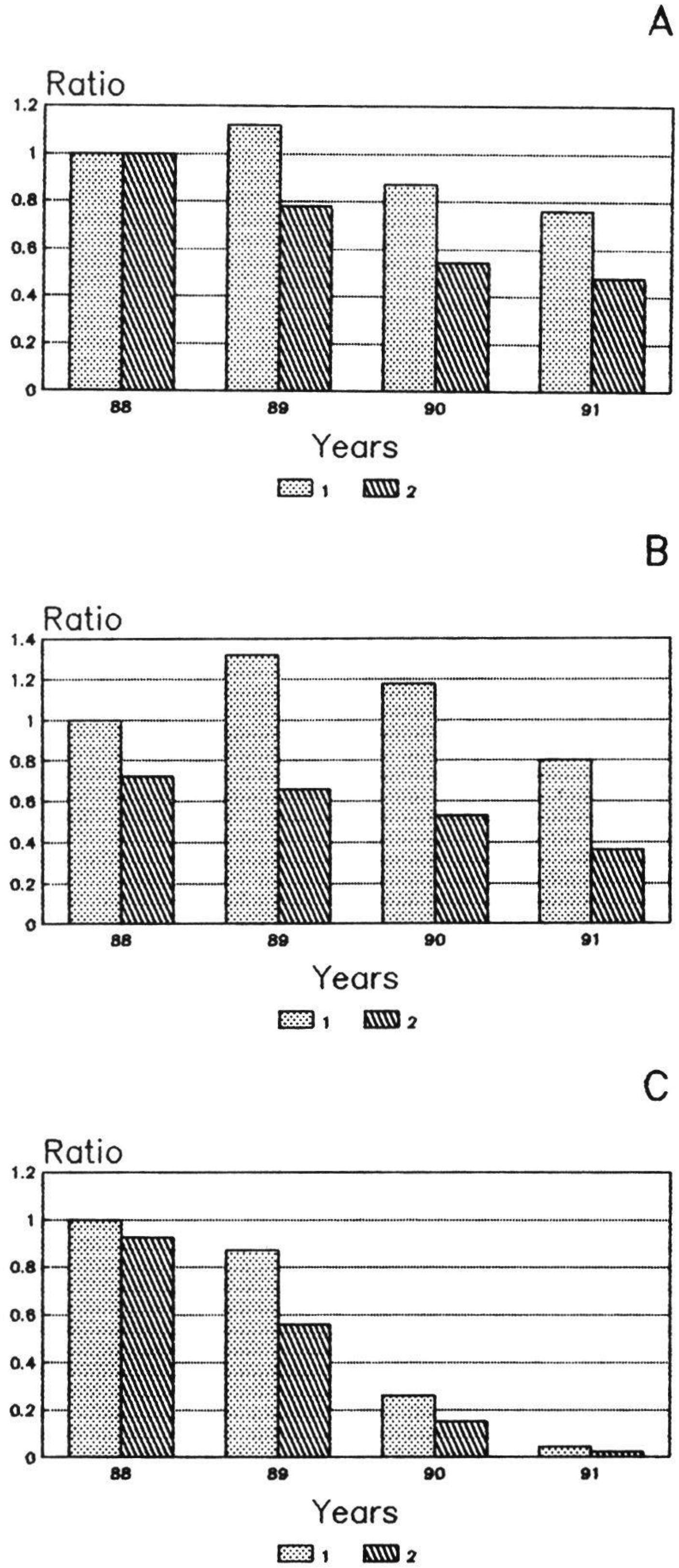

Fig. 7.1. Ratio of the total number of shoots in an experimental variant in a given year to: 1 = the total number of shoots in the variant in 1988, 2 = the total number of shoots in the control of the current year. Experimental variants: A = shading for the first half of the vegetative season, B = shading for the second half of the vegetative season, C = shading for the whole summer.

7.3.2. Changes on plots shaded for the first half of the vegetative season

In this variant of the shading experiment, the total number of species and floristic diversity decreased less sharply than in the above variant. Still, the total number of species decreased from 22 in the beginning to 17 by the end of the experiment, and floristic diversity from 8.3 species per plot to 5.3 (Table 7.2 and Fig. 7.1). The total number of shoots decreased from 2721 in the beginning to 2071 in the third year of the experiment, which is half that of the control (4334 shoots in the third year).

As in the previous case, least tolerant were *Antennaria dioica, Euphrasia ossica* and *Cerastium purpurescens. Antennaria dioica* is typical for ALH communities with low productivity, and therefore composed of small heliophytic plants. The decline of the annual semiparasitic *Euphrasia ossica* should obviously be connected with the deficiency of light, crucial for stimulation of seed germination in this group (GRIME 1981). An analysis of the relative coefficient of the seven species listed above, revealed a significant divergence in plant reactions to shading (Table 7.3). Thus, particularly *Anthoxanthum odoratum, Nardus stricta* and *Viola oreades* kept the same coefficient value for all three years and were therefore stable, whereas *Festuca ovina*, *Festuca varia* and *Gentiana djimilensis* gradually decreased in number, as in the all-summer shading variant. *Gentiana djimilensis* declined slower than the other two species.

Most curious was the behaviour exhibited by *Carex umbrosa*: its third year coefficient exceeded 1, meaning a considerable increase in shoot quantity compared with the control. Probably, being quite tolerant to shading as a wintergreen plant, this species becomes a superior competitor under severe shading while other species rapidly decline.

Shading during the first half of summer seriously influenced the development of generative shoots. Only three species, namely *Anthoxanthum odoratum, Festuca ovina* and *Erigeron venustus*, produced generative shoots, compared to 8 in the beginning.

7.3.3. Changes on plots shaded for the second half of the vegetative season

In this variant, general changes in the composition of the grassland were the same as under shading for the first half of the summer. The total number of species decreased insignificantly from 21 to 18, and floristic diversity dropped from 5.9 to 4.2 (Table 7.2 and Fig. 7.1). Only one species (*Ranunculus oreophilus*) produced generative shoots in the final year of the experiment. The total number of shoots was reduced from 1961 in the initial year to 1573 in the third year of experiment, a third of the control (4334 shoots in the third year) (Table 7.1).

In this variant, the relative coefficient for *Anthoxanthum odoratum* suggests a sharper decline in the number of shoots for three years than in the first half of the summer variant. *Anthoxanthum odoratum* is often considered as an early developing grass (e.g. GUBANOV et al. 1990), but results show that for vegetation of this species, the second half of summer is more crucial. The coefficient values of other species, as in the previous case, decreases. Only the coefficient of *Viola oreades* increased somewhat (K value for the third year is 2.65), which is a considerable rise in shoot number, in comparison with the control. The shoot quantity of *Carex umbrosa* did not change noticeably. Therefore, it may be concluded that shading for the first half of summer is more crucial for the early germinating *Viola oreades*, while for *Carex umbrosa* the second half of the summer is more important.

7.3.4. Changes in floristic diversity of ALH and FVG under shading

Results are generally similar to those obtained in previous shading experiments in ALHs (RABOTNOVA et al. 1992). ALHs are slightly richer in species (25.5 per variant in ALHs against 22.5 in FVGs), and average floristic diversity is doubled (14.6 species per plot against 7.1 species per plot respectively). It is interesting, that under severe shading (all-summer variant) ALHs proved less stable than FVGs, in which the total number of species declined by a factor of four during the experiment (from 27 to 7), and floristic diversity by 5.4 (from 14.0 to 2.6), whereas FVGs decreased only by half in total number of species (from 24 to 11), and by 4.7 in floristic diversity (from 8.5 to 1.8).

Therefore, it can be supposed that FVG species, which are adapted to communities dominated by the tall grass, *Festuca varia*, are in general more shade-tolerant than those of ALHs. ALH communities are formed under the extremely severe conditions of snow-free mountain crests (see chapter 1), and thus are composed of dwarf species which are very sensitive to any shading.

SUMMARY

Shading, cutting off more than 95% of light, seriously affected the growth of plants in alpine grasslands (FVG) in the Northwestern Caucasus. Many species failed to vegetate under harsh shading conditions, and therefore disappeared from the community. Comparing present results with those obtained in previous ALH shading experiments (RABOTNOVA et al. 1992), we found that FVGs appear more stable than ALHs. In the all-summer shading variant in FVGs, the total number of species decreased by a factor of two, whereas in ALHs, the total number of species decreased by a factor of four. Species, growing in FVG communities are less sensitive to shading than those in ALHs.

The most serious decline was observed under all-summer (three months) shading for three years. Only 46% of all species survived. All species decreased in shoot quantity by several times. The most tolerant species were ever- or winter-green plants like *Vaccinium vitis-idaea* and *Gentiana djimilensis*, and some partially winter-green grasses like *Nardus stricta, Anthoxanthum odoratum* and the stress-tolerant *Viola oreades*.

Shading during 1.5 months for the first or second half of the summer had a lesser effect on the community. In this case about 77% of the species survived after three experimental years. Still, some species especially sensitive to shading did not survive, among these were *Antennaria dioica* (a typical ALH species), *Minuartia recurva, Cerastium purpurascens,* annual *Euphrasia ossica, Campanula collina* and *Anthemis iberica*. The shoot quantity in most species declined considerably.

In the latter two variants, three species increased in number of shoots: *Festuca varia* in the first year of shading for the second half of summer, *Viola oreades* during all three years in the same variant, and in the variant, first half of summer, *Carex umbrosa*. This fact can be explained by the seasonal divergence of the active vegetation periods of these three species. Being obviously quite shade-tolerant, all of them possibly have advantages in competition for light over other members of the community. It seems that *Viola oreades* and *Festuca varia* need more light in the first half of the summer, probably because both tend to develop early. *Carex umbrosa*, on the contrary, probably finds better conditions for vegetation in the last half of the summer.

The number of generative shoots decreased more rapidly than that of vegetative ones. Thus most species stopped producing generative shoots under shading. Probably this feature of alpine plants is responsible for their inability to compete successfully for light against subalpine species at lower altitudes (TAPPEINER et al. 1989).

(ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands).