

Dynamics of two contrasted alpine communities in the Caucasus: results of 14-years permanent plot observations

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Abstract. Fluctuation and successional dynamics were studied in alpine lichen heath (ALH, winter snow free community) and snowbed community (SBC) in the Teberda Reserve, the Northwest Caucasus. Shoot numbers of each species were counted on 80 permanent plots for 14 years. Mean temporal variation coefficients were significantly bigger for generative shoot numbers than for total shoot numbers in both communities. All studied ALH species had coefficients of variation for total shoot number of less than 60%, but 5 of 20 species in SBC exceeded this value. A significant positive correlation coefficient was obtained between spatial and temporal variation for combined data and for total shoot numbers in SBC. As a whole, dominants were more stable than less abundant species in both communities. Most of the species in SBC showed positive correlations with each other (*Festuca ovina*, *Carum meifolium*, *Pedicularis nordmanniana*, *Luzula multiflora*, *Anthoxanthum odoratum*, *Corydalis conorhiza*, *Gentiana pyrenaica*, *Festuca brunnescens*, *Phleum alpinum*). Several species of ALH and SBC showed a significant linear trend for the period of observation. A positive trend (significant increase of shoot number) was found in 8 species in SBC, but *Catabrosella variegata* demonstrated a significant decrease in population density. Many fewer (5 from 19 studied species) ALH species showed an increase in shoot numbers. Only *Trifolium polyphyllum* decreased population density in ALH. Increased abundance of meadow species may be connected with global climatic changes or with a long-term response to the ending of grazing. According to autocorrelation analysis all species can be divided into two groups. The first group (most of the species in both communities) included species without any significant correlation coefficient for all temporal lags. The other group included species that had

significant positive correlation coefficients for lag 1 year. More species from SBC demonstrated such conservative dynamics.

Key words: Alpine snowbed community, alpine lichen heath, fluctuations, succession, permanent plots, global change, Teberda Reserve

Introduction

Alpine plant communities are more sensitive to climatic changes than lowland ones, and vertical migrations of phytogeographical belts for 200-400 m took place in the Caucasus during the Holocene (Tushinskii 1957, 1962, Shcherbakova 1973). Therefore alpine ecosystems have attracted significant scientific interest as models for studying plant response to global changes such as CO₂ and increasing temperature (Chapin and Körner 1994, Körner 1995, Diemer and Körner 1998, Grabherr *et al.* 1995, Schappi and Körner 1996, 1997, Körner *et al.* 1997). However, there are few direct observations of vegetation dynamics during recent decades (Khrantsov 1982, Lesica and Steele 1996).

Snow cover is the main factor that determines plant cover and structure in humid alpine areas such as the Northwest Caucasus (Walter 1975, Nefed'eva and Yashina 1985, Grishina *et al.* 1986). Communities on leeward slopes with great snow accumulation (4-6 m and more) are protected from strong winter frost, but they have a short growth season determined by snowmelt dates. On the other hand, snowfree windward slopes are occupied by alpine heaths and grasslands, which develop under deep winter freezing. The most productive alpine meadows develop on slopes with moderate snow accumulation (2-3 m) (Onipchenko 1990).

Dynamics and spatial structure of plant communities may be interrelated. For model communities with a competitive hierarchy, Lehman and Tilman (1997) showed that less-abundant species had more temporal variation and more aggregated spatial distributions. But there is no empirical evidence for these ideas.

Our previous investigations showed that snowfree alpine communities in the Caucasus were more stable during recent millennia than the snowbed communities (Pavlova and Onipchenko 1992, Blinnikov 1994) due to chang-

ing precipitation and snow depth. We can hypothesise that the same is true for shorter time periods. The aims of the present paper were to compare dynamics of two contrasted communities (snowfree alpine lichen heath and snowbed community) during 14 years of permanent plot observations in the Teberda National Biosphere Reserve (Russia). We considered the following questions:

- 1) Are there differences temporal variability of shoot density between the communities?
- 2) Are spatial and temporal variability correlated?
- 3) Can we distinguish groups of species according their dynamic behaviour?
- 4) Is there any correlation between climatic parameters and species abundance?
- 5) Have any species a significant overall trend?
- 6) Are there short-term cycles in species dynamics and are autocorrelation functions similar for different species and communities?

Methods

Study area and site description

The study area is situated on the Mt. Malaya Khatipara, Teberda National Biosphere Reserve, Karachaevo-Cherkessian Republic, the Northwest Caucasus, Russia (43° 27' N, 41° 41' E). Permanent plots were located in two ecologically contrasted communities, namely alpine lichen heath and snow bed community, at an elevation 2,750 - 2,800 m above sea level.

The alpine lichen heath (ALH) is a low-productivity community dominated by fruticose lichens (mainly *Cetraria islandica*) and low (up to 10 cm) graminoids and forbs. In the region of study, such communities occupy southern windward slopes and crests with little (< 0.3 m) or no winter snow accumulation. The studied communities belong to the subassociation *Pediculari comosae - Eritrichietum caucasici oxytropidetosum kubanensis* of the alliance *Anemonion speciosae* Minaeva 1987 (*Caricetea curvulae* Br.-Bl. 1948) (Onipchenko *et al.*, 1987). The total lichen dry biomass is about 440 g/m², the total aboveground dry biomass of vascular plants is 110 g/m², belowground - 480 g/m². Detailed descriptions of the study site and the alpine lichen heath of the Teberda reserve can be found in Grishina *et al.* (1986), Rabotnov (1987), and Onipchenko (1994a, b).

Snowbed communities (SBC) occupy depressions and bottoms of glacial cirques ("kars") with heavy snow accumulation (4 metres and more). Therefore they have short a vegetative season (about 2 - 2,5 months) from the end of July to September. Short rosette and dwarf trailing plants (*Sibbaldia procumbens*, *Minuartia aizoides*, *Gnaphalium supinum*, *Taraxacum stevenii*) and *Nardus stricta* are dominants here. In some plots *Sibbaldia procumbens* is an absolute dominant. Height of most plants is 2-3 cm only. This community type belongs to association *Hyalopoo ponticae - Pedicularietum nordmannianae*

(Rabotnova 1987), *Sibbaldion* Rabotnova 1987 (*Salicetea herbaceae* Br.-Bl. 1947). Aboveground vascular plant biomass is about 129 g/m², belowground - 944 g/m². Corresponding values for necromass are 184 and 592 g/m² (Onipchenko 1990).

Field methods

Two transects 0.5 x 5 m were established in each community. They were divided into 40 plots 25 x 25 cm. Total number of plots was 80 for each community. Plots were fixed by pegs and fishing line. We counted shoots (vegetative and generative) as well as juveniles on the plots from 1986 to 1999. Counting took place at approximately the same time each year, at the end of July -early August for ALH and in the middle of August for SBC.

Climatic parameters were obtained from the nearest meteorological station (Teberda, 1328 m a.s.l.). We used monthly mean temperature, mean minimal (mean amongst daily minima) and mean maximal (mean amongst daily maximums) temperature and sum of precipitation. Data for current year (from January to June) and the previous year (from January to December) were used.

Statistical analysis

To compare the rate of fluctuation between species we used variation coefficient (standard deviation x 100% / mean value). The same coefficient was used to compare temporal and spatial (on 25 x 25 cm plots) variation for the species. Only species with minimal shoot number of 10 were involved in the calculation.

Due to different distribution features of the studied species, we use nonparametric (Spearman) correlation coefficient to estimate the relationships between different species dynamics and the possible influence of weather on shoot number dynamics. We analysed four correlation matrices. They represented correlation coefficients 1) among ALH species, 2) among SBC species, 3) between common ALH and SBC species 4) among ALH, SBC and weather conditions. Correlation diagrams were drawn to show significant positive correlations between species.

To assess the direction and degree of change in annual shoot counts we tested for presence of a linear trend using a standard technique (Zar 1999). For each species in every community we calculated Pearson's correlation coefficient r between the experiment's year number and total number of the species' shoots in each year. A strong negative correlation implies a strong decrease in the shoot density over the years, while strong positive one - a strong increase. Statistical significance of the linear trend was obtained by calculating t-statistic from the formula:

$$t = |r/s_r|$$

where r is Pearson's correlation coefficient between the year number and the total number of the species' shoots in each year, s_r - standard error of r , and the degrees of freedom are $n-$

2 (n=14 years). We compared t with critical values for the two-tailed t distribution (Zar 1999).

To estimate possible temporal autocorrelation we calculate autocorrelation functions (relationships between correlation coefficients and lags) for each studied species. Minitab 11.12 for Windows was used for the calculations.

Results

Shoot density variations

Shoot density varied for all studied species in both communities (Table 1). Mean temporal variation coefficients were significantly bigger for generative shoot numbers than for total shoot numbers in both communities (ALH: 74,0% for generative shoots and 27,4% for total shoot numbers, $p=0,026$; SBC 82,9% and 42,1%, $p = 0,001$). ALH species shoot density varied significantly less than that for SBC ($p=0,035$), but there were no differences in generative shoot variations between the communities. All studied ALH species had variation in total shoot number of less than 60%, but 5 out of 20 species in SBC exceeded this value.

A significant positive correlation coefficient was obtained between spatial and temporal variation for combined data (n=60, $r= 0,34$, $p<0,001$) and for total shoot numbers in SBC (n=20, $r=0,52$, $p<0,05$). Two cushion plants (*Arenaria lychnidea*, *Minuartia circassica*) were among obvious exceptions to the overall trend: the species had very aggregated spatial distributions but they were very stable temporally (Table 1).

As a whole, dominants (ALH: *Anemone speciosa*, *Campanula tridentata*, *Carex umbrosa*, *Festuca ovina*, *Antennaria dioica*, *Trifolium polyphyllum*, SBC: *Gnaphalium supinum*, *Minuartia aizoides*, *Sibbaldia procumbens*, *Taraxacum stevenii*) were more stable than less abundant species in both communities. Mean variation coefficient for ALH dominants was 18% versus 32% for nondominants, $p=0.0052$, corresponding values for SBC species were 22% and 47%, $p=0.0017$.

Species groups according to their dynamic behaviour

Analysis of correlation matrix (not shown) allowed as to distinguish groups of species with similar dynamic behaviour. Several small correlation groups were obtained in ALH (Fig. 1). *Eritrichium caucasicum*, *Gentiana pyrenaica*, *Agrostis vinealis*, and *Luzula spicata* formed the largest group at a significance of $p=0,01$. *Festuca ovina*, *Minuartia circassica* and *Erigeron alpinum* formed on other group, while *Carum caucasicum* and *Arenaria lychnidea* were positively correlated with each other. But there were many positive correlations at a lower level of significance ($0,05>p>0,01$) for the species between the groups; thus the species of those three groups did not show major differences in dynamics. Completely different shoot dynamics was shown by *Trifolium*

polyphyllum. It species had negative correlations ($p<0.05$) with 3 species of the second group (*Minuartia circassica*, *Festuca ovina*, *Erigeron alpinum*).

A completely different picture was obtained for SBC where most of the species showed positive correlations with each other (Fig. 1). Nine species had significant positive correlations with the other eight (*Festuca ovina*, *Carum meifolium*, *Pedicularis nordmanniana*, *Luzula multiflora*, *Anthoxanthum odoratum*, *Corydalis conorhiza*, *Gentiana pyrenaica*, *Festuca brunnescens*, *Phleum alpinum*). Four other species comprised a second group in SBC (*Carex oreophila*, *Taraxacum stevenii*, *Minuartia aizoides*, *Gnaphalium supinum*). It is interesting to note that there were no significant negative correlations among SBC species at $p<0,01$. SBC species had more interrelated dynamics than ALH species.

There were three species (*Agrostis vinealis*, *Festuca ovina* and *Gentiana pyrenaica*) common to ALH and SBC. We calculated Spearman correlation coefficient for shoot numbers of the species between the two communities. A significant positive correlation coefficient was obtained for *Festuca ovina* ($r = 0,705$, $p < 0,01$) only.

Correlation between species and weather conditions

The correlation matrix for 62 species shoot numbers and 54 weather parameters consisted of 3348 values (data have not shown). We obtained 10 (0.3%) significant values at $p<0.001$, 34 (1.0%) values at $p<0.01$, and 171 (5.1%) values at $p<0.05$. The two last values are close to random estimation (Type I error), so we consider the first group of values only (Table 2). Several SBC species (*Anthoxanthum odoratum*, *Luzula multiflora*, *Phleum alpinum*) showed positive correlation with minimal temperature in the previous October. A warm autumn can facilitate shoot development of these species in the following year. Precipitation in May of the previous year correlated positively with *Anemone speciosa* generative shoot numbers. Generative shoots of *Eritrichium caucasicum* correlated negatively with precipitation in April of the current year.

Trends in species dynamics

Several species of ALH and SBC showed a significant linear trend for the period of observation (Table 3). A positive trend (significant increase of shoot number) was found for 8 species in SBC, most of them (except *Corydalis conorhiza* and *Hyalopoa pontica*) more typical for more productive alpine meadows. One common SBC species (*Catabrosella variegata*) demonstrated a significant decrease in population density.

Many fewer (5 from 19 studied species) ALH species showed an increase in shoot numbers. Only one species (*Trifolium polyphyllum*) decreased population density in ALH.

Species	temporal mean	variability std	(n=14) CV, %	Spatial mean	variability std	(n=80) CV, %
Total shoot number						
Alpine lichen heath (ALH)						
<i>Agrostis vinealis</i>	46	23.6	52	0.43	1.6	381
<i>Anemone speciosa</i>	212	34.3	16	2.93	2.2	76
<i>Antennaria dioica</i>	289	56.6	20	4.73	10.6	224
<i>Arenaria lychnidea</i>	116	24.8	21	1.41	8.2	579
<i>Campanula tridentata</i>	1522	240.3	16	18.54	10.3	55
<i>Carex umbrosa</i>	1541	374.9	24	16.23	9.3	57
<i>Carum caucasicum</i>	493	126.3	26	6.34	3.7	59
<i>Erigeron uniflorus</i>	19	6.1	32	0.31	1.0	308
<i>Eritrichium caucasicum</i>	358	128.4	36	2.98	4.2	140
<i>Festuca ovina</i>	7384	1838.1	25	109.26	53.0	48
<i>Gentiana pyrenaica</i>	997	319.5	32	10.99	13.1	119
<i>Helictotrichon versicolor</i>	798	100.6	13	10.46	10.3	98
<i>Luzula spicata</i>	105	21.2	20	1.23	3.4	276
<i>Minuartia circassica</i>	40	13.6	34	0.71	5.2	728
<i>Pedicularis caucasica</i>	18	9.5	54	0.20	0.9	467
<i>Pedicularis comosa</i>	50	17.0	34	0.24	0.5	204
<i>Trifolium polyphyllum</i>	353	22.2	6	2.30	5.8	253
<i>Veronica gentianoides</i>	21	6.9	33	0.19	0.7	371
Snow bed community (SBC)						
<i>Agrostis vinealis</i>	777	179.7	23	10.05	15.0	150
<i>Anthoxanthum odoratum</i>	602	309.9	51	13.26	25.6	193
<i>Carex atrata</i>	119	18.5	15	1.50	3.9	257
<i>Carex oreophila</i>	1700	335.8	20	16.31	16.3	100
<i>Carum meifolium</i>	507	408.9	81	9.39	16.0	170
<i>Catabrosella variegata</i>	1852	424.0	23	15.09	12.1	80
<i>Corydalis conorhiza</i>	453	469.3	104	4.71	7.5	160
<i>Festuca brunnescens</i>	180	141.6	79	4.86	17.5	360
<i>Festuca ovina</i>	243	97.5	40	3.98	8.3	210
<i>Gentiana pyrenaica</i>	19	15.0	81	0.50	2.6	521
<i>Gnaphalium supinum</i>	2772	553.9	20	32.01	63.0	197
<i>Hyalopoa pontica</i>	23	14.0	62	0.24	0.8	354
<i>Luzula multiflora</i>	244	89.0	36	3.25	10.1	310
<i>Minuartia aizoides</i>	6827	1881.9	28	66.89	43.3	65
<i>Nardus stricta</i>	7885	2863.2	36	100.41	86.9	87
<i>Pedicularis nordmanniana</i>	687	279.9	41	9.20	11.5	125
<i>Phleum alpinum</i>	699	276.4	40	11.11	14.7	132
<i>Potentilla crantzii</i>	1122	275.5	25	14.80	25.0	169
<i>Sibbaldia procumbens</i>	6915	1376.3	20	86.09	43.0	50
<i>Taraxacum stevenii</i>	2771	520.5	19	27.84	16.2	58
Generative shoot number						
Alpine lichen heath (ALH)						
<i>Anemone speciosa</i>	65	12.8	20	0.93	1.2	130
<i>Campanula tridentata</i>	346	104.0	30	6.24	3.9	63
<i>Carex umbrosa</i>	38	46.5	121	0.19	0.5	283
<i>Carum caucasicum</i>	118	18.4	16	1.65	1.5	88
<i>Eritrichium caucasicum</i>	22	13.0	60	0.04	0.2	510
<i>Festuca ovina</i>	130	109.0	84	1.68	1.9	112
<i>Gentiana pyrenaica</i>	90	37.0	41	0.81	1.4	174
<i>Helictotrichon versicolor</i>	22	30.5	136	0.28	0.7	259
Snow bed community (SBC)						
<i>Anthoxanthum odoratum</i>	41	39.6	97	1.78	3.8	215
<i>Carex oreophila</i>	203	67.8	33	2.08	3.3	159
<i>Carum meifolium</i>	18	13.4	76	0.34	0.8	231
<i>Catabrosella variegata</i>	64	90.9	141	0.03	0.2	628
<i>Corydalis conorhiza</i>	39	37.2	94	0.28	0.6	231
<i>Gnaphalium supinum</i>	94	107.1	114	0.79	1.7	218
<i>Luzula multiflora</i>	35	24.6	70	0.30	1.2	402
<i>Minuartia aizoides</i>	116	138.1	119	0.33	0.8	234
<i>Nardus stricta</i>	85	112.3	132	4.70	9.4	199
<i>Pedicularis nordmanniana</i>	141	85.9	61	2.26	2.9	127
<i>Phleum alpinum</i>	51	31.8	62	0.89	2.0	221
<i>Potentilla crantzii</i>	35	27.1	78	0.10	0.4	439
<i>Sibbaldia procumbens</i>	180	74.6	41	4.18	4.3	102
<i>Taraxacum stevenii</i>	210	86.5	41	1.51	2.1	142

Table 1. Parameters of spatial and temporal variability. Spatial variability parameters were counted for 80 plots (25 x 25 cm) in 1998 year. Std – standard deviation, CV – variation coefficient.

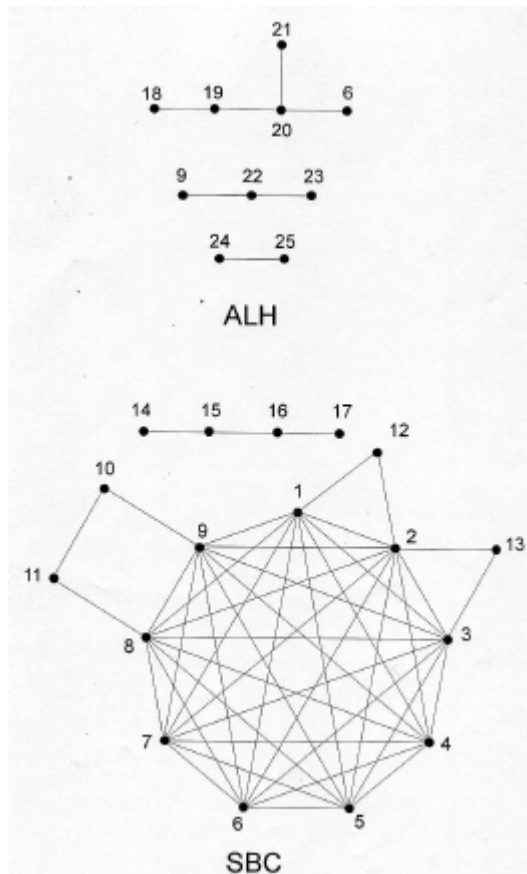


Fig. 1. Correlation diagrams for groups of species with similar dynamic behaviour. Values of the positive Spearman correlation coefficient (significance level $p < 0.01$) are indicated by solid lines within communities only. Species: 1 – *Carum meifolium*, 2 – *Pedicularis nordmanniana*, 3 – *Luzula multiflora*, 4 – *Anthoxanthum odoratum*, 5 – *Corydalis conorhiza*, 6 – *Gentiana pyrenaica*, 7 – *Festuca brunnescens*, 8 – *Phleum alpinum*, 9 – *Festuca ovina*, 10 – *Potentilla crantzii*, 11 – *Nardus stricta*, 12 – *Hyalopoa pontica*, 13 – *Sibbaldia procumbens*, 14 – *Carex oreophila*, 15 – *Taraxacum stevenii*, 16 – *Minuartia aizoides*, 17 – *Gnaphalium supinum*, 18 – *Veronica gentianoides*, 19 – *Agrostis vinealis*, 20 – *Eritrichium caucasicum*, 21 – *Luzula spicata*, 22 – *Minuartia circassica*, 23 – *Erigeron alpinum*, 24 – *Arenaria lychnidea*, 25 – *Carum caucasicum*.

Autocorrelation analysis

According to their autocorrelograms (data are not shown) all species can be divided into two groups. The first group (most of the species in both communities) showed no significant correlation coefficient for any temporal lag (from 1 to 10 years). The other group included species with more conservative dynamics, namely they had significant positive correlation coefficients for lag 1 year. That is, next year's number of shoots depended on current year shoot density. Nine species (3 from ALH and 6 from SBC) belonged to this group (Table 4), suggesting that relatively more species from the snow bed community demonstrated such conservative dynamics.

Discussion

Shoot density variation

We obtained 3 main results: temporal variation for total shoot number was lower then for generative shoots, species in SBC fluctuated more than in ALH, and spatial and temporal variation were positively correlated for most of the species, except cushion plants. Great interannual variation in generative shoot number has also been shown in long-term observation in ALH (Golikov and Onipchenko 1999), as well as for *Bromopsis variegata* in subalpine meadows (Khramtsov 1982). Between-year variation in seed production is higher than plant density variation in alpine areas (Lesica and Steel 1996, Logvinenko and Onipchenko 1999).

Abundant nonclonal (*Anemone speciosa*, *Campanula tridentata*) as well as clonal (*Festuca ovina*, *Carex umbrosa*, *Carex oreophila*) and cushion (*Arenaria lychnidea*, *Minuartia circassica*) species showed relatively low temporal shoot density variation. Low rate of temporal variation was observed for *Carex curvula* in Alps (Erschbamer *et al.* 1998).

Our results supported the idea that dynamics and spatial structure of plant communities may

Species	Com	Sh	Weather parameter	Cor. Coef.
<i>Anthoxanthum odoratum</i>	SBC	G	Mean temp. in previous year October	0.81
<i>Anthoxanthum odoratum</i>	SBC	G	Mean minimal temp. in previous year October	0.83
<i>Corydalis conorhiza</i>	SBC	G	Mean temp. in current year January	-0.76
<i>Luzula multiflora</i>	SBC	S	Mean minimal temp. in previous year October	0.77
<i>Phleum alpinum</i>	SBC	S	Mean minimal temp. in previous year October	0.76
<i>Sibbaldia procumbens</i>	SBC	G	Precipitation in current year April	0.79
<i>Anemone speciosa</i>	ALH	G	Precipitation in previous year May	0.79
<i>Eritrichium caucasicum</i>	ALH	G	Precipitation in current year April	0.78
<i>Eritrichium caucasicum</i>	ALH	G	Mean temp. in previous year December	-0.76
<i>Helictotrichon versicolor</i>	ALH	S	Mean temp. in current year February	-0.83

Table 2. Significant Spearman correlation coefficients ($p < 0.001$) between shoot numbers and weather parameters. Abbreviations: Sh. – shoots: G - generative, S - sum of vegetative, generative and juvenile shoots; Com: SBC - snow bed community, ALH - alpine lichen heath, temp. – temperature.

Species	Sh.	Com.	r	B	steB	P
<i>Anthoxanthum odoratum</i>	S	SBC	0.86	63.78	10.87	0.001
<i>Carum meifolium</i>	S	SBC	0.87	85.23	13.82	0.001
<i>Catabrosella variegata</i>	S	SBC	-0.55	-55.49	24.49	0.043
<i>Corydalis conorrhiza</i>	S	SBC	0.59	65.84	26.22	0.028
<i>Festuca brunnescens</i>	S	SBC	0.95	32.13	3.07	0.001
<i>Festuca ovina</i>	S	SBC	0.63	14.72	5.22	0.016
<i>Gentiana pyrenaica</i>	S	SBC	0.79	2.83	0.64	0.001
<i>Hyalopoa pontica</i>	S	SBC	0.72	2.42	0.67	0.004
<i>Luzula multiflora</i>	S	SBC	0.67	14.26	4.56	0.009
<i>Anthoxanthum odoratum</i>	G	SBC	0.74	7.04	1.83	0.003
<i>Carum meifolium</i>	G	SBC	0.71	2.27	0.65	0.005
<i>Catabrosella variegata</i>	G	SBC	-0.60	-13.05	5.01	0.024
<i>Nardus stricta</i>	G	SBC	0.60	16.16	6.19	0.023
<i>Arenaria lychnidea</i>	S	ALH	0.60	3.54	1.38	0.025
<i>Campanula tridentata</i>	S	ALH	0.62	35.5	13.01	0.018
<i>Erigeron alpinus</i>	S	ALH	0.82	1.19	0.24	0.001
<i>Festuca ovina</i>	S	ALH	0.85	372.22	67.40	0.001
<i>Minuartia circassica</i>	S	ALH	0.92	2.97	0.37	0.001
<i>Trifolium polyphyllum</i>	S	ALH	-0.69	-3.66	1.11	0.007

Table 3. Parameters of linear trends. Abbreviations: Sh. – shoots; G - generative, S - sum of vegetative, generative and juvenile shoots; Com: SBC - snow bed community, ALH - alpine lichen heath, r – correlation coefficient, B – linear regression coefficient, steB – standard error of B, P – error probability.

Species	Community	R	t
<i>Anthoxanthum odoratum</i>	SBC	0.61	2.27
<i>Festuca brunnescens</i>	SBC	0.70	2.62
<i>Festuca ovina</i>	SBC	0.59	2.20
<i>Gentiana pyrenaica</i>	SBC	0.54	2.04
<i>Hyalopoa pontica</i>	SBC	0.65	2.42
<i>Pedicularis nordmanniana</i>	SBC	0.53	2.00
<i>Carex umbrosa</i>	ALH	0.58	2.17
<i>Erigeron alpinus</i>	ALH	0.66	2.45
<i>Gentiana pyrenaica</i>	ALH	0.52	1.94

Table 4. Significant autocorrelation coefficients for lag 1 year. R – correlation coefficient, t – t-criteria value (n=13)

be interrelated. The behaviour of SBC species was more consistent with the competitive hierarchy model of Lehman and Tilman, (1997) than that of the ALH species. We may speculate that a competitive hierarchy plays a more important role in SBC than in ALH, where facilitation between dominants and subordinate species has been shown (Aksenova *et al.* 1998).

Inter-year dynamics of the communities can be decomposed into two components: fluctuations (non directional changes, see Miles 1979) and successional (directed) trends.

Rabotnov (1972) classified fluctuations in grasslands into 3 main types: 1) "hidden" – composition and structure of communities are stable, only quantitative changes in shoot dynamics take place; 2) "oscillations" – several dominants alternate according to climatic vari-

ations between years; 3) "demutations" – cycles including local disturbance and recovery. As both studied communities kept their structure and composition through the whole period of observation, we may consider the fluctuation as "hidden" according to this classification.

About half of the studied species showed a progressive increase in shoot density during the study period. This trend was more common among SBC species, and the species concerned are more widespread in alpine meadows than in SBC (Onipchenko 1994). Moen and Oksanen (1998) considered snow bed communities in Sweden as secondary communities, developed under strong grazing. Our SBC were grazed by domestic ungulates until 1943 and they still show some signs of former overgrazing (high abundance of low palatable species - *Sibbaldia procumbens*, *Nardus stricta*). The increase of meadow species abundance may therefore be the result of secondary succession after the ending of grazing.

Other possible explanations of the succession trends may be connected with current climate change. We have found a positive trend for minimal October temperature for Teberda meteorological station during last 19 years (Blinkova and Onipchenko 2001). But only few species demonstrated positive correlation with October temperature (Table 2). The list of the species with such correlations and linear trends overcover only slightly (compare Table 2 and 3).

Most of the SBC species that had concordant dynamic behaviour (Fig. 1) had a significant linear trend and increased their shoot numbers during the observation period, so the successional trend is more obvious in this community.

These results are consistent with hypothesis that the snowfree alpine communities in the Caucasus are more stable than snowbed communities for short time periods. The same is true for longer periods (hundred years and millennia) (Pavlova and Onipchenko 1992, Blinnikov 1994).

The short period of observation (14 years) did not allow us to evaluate cyclic dynamics of alpine species. Cycles, if they exist, appear to be longer than 10 years. Further observations are necessary to study this aspect of alpine plant population dynamics.

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References

- Aksenova, A.A., Onipchenko, V.G. and Blinnikov, M.S. 1998: Plant interactions in alpine tundra: 13 years of experimental removal of dominant species. *Ecoscience*, **5**: 258-270.
- Blinkova, O.V. and Onipchenko, V.G. 2001: Inter-year dynamics of alpine lichen heath. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otd. Biol.*, **106**: 66-73.
- Blinnikov, M.S. 1994: Phytolith analysis and holocene dynamics of alpine vegetation. In *Experimental investigation of alpine plant communities in the Northwestern Caucasus* (eds. V.G. Onipchenko and M.S. Blinnikov), pp. 23-40. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich, 115.
- Chapin, F.S. and Körner, Ch. 1994: Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. *Trends in Ecology and Evolution*, **9**: 45-47.
- Diemer, M., and Körner, Ch. 1998: Transient enhancement of carbon uptake in an alpine grassland ecosystem under elevated CO₂. *Arctic and Alpine Research*, **30**: 381-387.
- Erschbamer, B., Buratti, U. and Winkler J. 1998: Long-term population dynamics of two *Carex curvula* species in the Central Alps on native and alien soils. *Oecologia*, **115**: 114-119.
- Golikov, K.A., and Onipchenko, V.G. 1999: Influence of meteorological factors on generative shoot dynamics in alpine lichen heath. *Trudy Teberdinskogo gosudarstvennogo biosfernogo zapovednika*, **15**: 64-72.
- Graherr, G., Gottfried, M., Gruber A. and Pauli, H. 1995: Patterns and current changes in alpine plant diversity. In *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (eds. F.S. Chapin and Ch. Körner), pp.167-181 Springer, Berlin.
- Grishina, L.A., Onipchenko, Makarov, M.I. 1986: Composition and structure of alpine heath biogeocoenosis [Sostav i struktura biogeocenzov alpijskikh pustoshei]. Moscow univ.press, Moscow.
- Khramtsov, V.N. 1982: Productivity of *Bromopsis variegata* (Poaceae) in plant communities of Teberda Reserve. *Botanicheskii Zhurnal*, **67**: 951-959.
- Körner, Ch. 1995: Alpine plant diversity: a global survey and functional interpretations. In *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (eds. F.S. Chapin and Ch. Körner), pp. 45-62. Springer, Berlin.
- Körner, Ch., Diemer, M., Schappi, B., Niklaus, P. and Arnone, J.A. 1997: The responses of alpine grassland to four seasons of CO₂ enrichment: a synthesis. *Acta Oecologica*, **18**: 165-175.
- Lehman, C.L. and Tilman, D. 1997: Competition in spatial habitats. *Spatial ecology: The role of space in population dynamics and interspecific interactions* (eds. D. Tilman and P. Kareiva), pp. 185-203. Princeton Univ. Press, Princeton.
- Lesica, P. and Steele, B.N. 1996: A method for monitoring long-term population trends: an example using rare arctic-alpine plants. *Ecological Applications*, **6**: 879-887.
- Logvinenko, O.A. and Onipchenko, V.G. 1999: Seed productivity of alpine plants. *Trudy Teberdinskogo gosudarstvennogo biosfernogo zapovednika*, **15**: 51-63.
- Miles, J. 1979: Vegetation dynamics . Chapman and Hall, London.
- Moen, J. and Oksanen, L. 1998: Long-term exclusion of folivorous mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation ecosystems. *Oikos*, **82**: 333-346.
- Nefed'eva, E.A. and Yashina, A.V. 1985: Role of snow cover in landscape differentiation [Rol' snezhnogo pokrova v differentsiatsii landshaftnoi sfery]. Nauka, Moscow.
- Onipchenko, V.G. 1990: Phytomass of alpine communities in the Northwest Caucasus. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otd. Biol.*, **95**: 52-62.
- Onipchenko, V.G. 1994a: Study area and general description of the investigated communities. In *Experimental investigation of alpine plant communities in the Northwestern Caucasus* (eds. V.G. Onipchenko and M.S. Blinnikov), pp. 6-22. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich, 115.
- Onipchenko, V.G. 1994b: The structure and dynamics of alpine plant communities in the Teberda Reserve, the Northwestern Caucasus. *Oecologia Montana*, **3**: 40-50.
- Onipchenko, V.G., Minaeva, T.Y. and Rabotnova, M.V. 1987: On syntaxonomy of alpine plant communities in Teberda Reserve. Manuscript VINITI N 1675-87
- Pavlova, I.V. and Onipchenko, V.G. 1992: Holocene dynamics of alpine vegetation in the Northwest Caucasus. In *Istoricheskaya ekologiya dikikh I domashnikh kopytnykh. Istoriya pastbishchnykh ekosistem* (ed. L.G. Dinesman), pp. 109-129. Nauka, Moscow.
- Rabotnov, T.A. 1972: Studies of fluctuation (inter-year dynamics) of phytocoenoses. *Polevaya geobotanica*, **4**: 95-136
- Rabotnov, T.A. (ed.) 1987: Biogeocoenoses of alpine heaths (NW Caucasus). [Biotsenosy alpijskikh pustoshei]. Nauka, Moscow.
- Schappi, B. and Körner, Ch. 1996: Growth responses of an alpine grassland to elevated CO₂. *Oecologia*, **105**: 43-52.
- Schappi, B., and Körner, Ch. 1997: In situ effects of elevated CO₂ on the carbon and nitrogen status of alpine plants. *Functional Ecology*, 1997, **11**: 290-299.
- Shcherbakova, E.M. 1973: Old glaciation in the Great Caucasus [Drevnee oledenenie Bol'shogo Kavkaza]. Moscow Univ. Press, Moscow.
- Tushinskii, G.K. 1957. Geomorphological features of Teberda Reserve. *Trudy Teberdinskogo gosudarstvennogo zapovednika*, **1**: 3-49.

- V. G. Onipchenko, O. V. Blinkova, A. A. Zakharov, & M. A. Abzeeva
- Tushinskii, G.K. 1962: Rythms in glaciation and snowness in Teberda State reserve. *Trudy Teberdinskogo gosudarstvennogo zapovednika*, **4**: 57-71.
- Walter, H. 1975. Tundras, grasslands, temporal deserts. *Rastitel'nost' Zemnogo shara*, **3**, 430 pp.
- Zar, J.H. 1999: *Biostatistical Analysis*. 4-th edit. Prentice-Hall, Upper Saddle River, 929 pp.

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