

5.6. Fluctuations and trends in the dynamics of alpine lichen heath and snowbed communities (Onipchenko V.G., Golikov K.A., Blinkova O.V., Zakharov A.A. 2004 In: W.Winterhoff (ed.), Alpine ecosystems in the Northwest Caucasus Kluwer Academic Publishers, Dordrecht)

5.6.1. 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 & Körner 1994, Körner 1995, Diemer & Körner 1998, Grabherr et al. 1995, Schappi & Körner 1996, 1997, Körner et al. 1997). However, there are few direct observations of vegetation dynamics during recent decades (Khramtsov 1982, Lesica & Steele 1996).

Dynamics and spatial structure of plant communities may be interrelated. For model communities with a competitive hierarchy, Lehman & Tilman (1998) showed that less-abundant species had more temporal variation and more aggregated spatial distributions. But there is no empirical evidence for these ideas.

Alpine communities are greatly influenced by different types of natural and anthropogenic disturbances. Revegetation successions take a long period of time. That is why the study of recovery of disturbed alpine plant communities is of both theoretical and practical interest (Willard & Marr 1971, Brown et al. 1978, Urbanska 1986, 1995). But there are only few works based on the direct long-term field observations (Gadzhiev 1979 Frank & del Moral 1986, Roxburgh et al. 1988, Tsuyuzaki 1991). Wild boar digging occurs rather often in high altitude areas and therefore it may serve as a suitable model of animal and human impact on alpine communities.

The aims of the present chapter 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 Reserve. We considered the following aspects of inter-year dynamics: 1) comparison of temporal variability of shoot density between the communities; 2) correlation between spatial and temporal variability; 3) separation of groups of species according to their dynamic behaviour; 4) correlation between climatic parameters and species abundance; 5) linear trends; 6) short-term cycles in species dynamics and autocorrelation functions. As a special aspect we studied revegetation dynamics of alpine lichen heath after wild boar digging.

5.6.2. Methods

Two transects 0.5 x 5 m were established in each community. They were divided into 40 plots of 25 x 25 cm. The total number of plots was 80 for each community. 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 or 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 daily minima) and mean maximal (mean daily maxima) temperatures and sum of precipitation. Data for the current year (from January to June) and the previous year (from January to December) were used.

We found some patches with a total area of about 5 square meters dug up by wild boars (*Sus scrofa* L.) in the autumn of 1980. Wild boars dug up the turf horizon of soil extracting apparently large roots of *Carum caucasicum*, *Campanula tridentata* and *Trifolium polyphyllum*. Most of the soil surface was deprived of plants and that led to the surface frost activity damaging seedlings and young plants. Five permanent plots of 25x25 cm were set up on these patches. Twenty undisturbed plots of the same size were taken as a control. Data have been collected annually during 20 years since 1981 in July and August (Onipchenko & Golikov 1996). The percent cover of vascular plants, lichens and bryophytes was recorded, as well as the percentage of bare soil surface. The number of juveniles and the density of vegetative and generative shoots were calculated for each vascular plant species.

Due to different distribution features of the studied species, we use nonparametric (Spearman) correlation coefficients 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). To estimate possible temporal autocorrelation we calculate autocorrelation functions (relationships between correlation coefficients and lags) for each studied species (Onipchenko et al. 2001).

5.6.3. Variation in shoot density

Shoot density varied for all studied species in both communities (Table 5.20, 5.21, Fig. 5.33). 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%, $p = 0.001$). In 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 showed variation in total shoot number of less than 60%, but 5 out of 20 species in SBC exceeded this value (Onipchenko et al. 2001).

A significant positive correlation coefficient was obtained between spatial and temporal variation for the 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 the obvious exceptions to the overall trend: the species had very aggregated spatial distributions but they were very stable temporally (Table 5.20).

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%, $p=0.0017$.

So, we obtained 3 main results: 1) the temporal variation for total shoot number was lower than for generative shoots, 2) species in SBC fluctuated more than in ALH, and 3) spatial and temporal variation were positively correlated for most of the species, except in cushion plants. Great interannual variation in generative shoot numbers has also been shown in long-term observation in ALH (Golikov & Onipchenko 1999), as well as for *Bromus variegatus* in subalpine meadows (Khrantsov 1982). Between -year variation in seed production is higher than variation in plant density in alpine areas (Lesica & Steel 1996, Logvinenko & Onipchenko 1999).

Table 5.20. Parameters of spatial and temporal variability of total shoot numbers. Spatial variability parameters were counted for 80 plots (25 x 25 cm) in 1998 year. Std - standard deviation, CV - variation coefficient. (from Onipchenko et al. 2001 with permission of *Oecologia Montana*)

Species	temporal variability (n=14)			Spatial variability (n=80)		
	mean	std	CV,%	mean	std	CV,%
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 caucasicum</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	109.3	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

Table 5.21. Parameters of spatial and temporal variability of generative shoots. (see Table 5.20 for abbreviations). (from Onipchenko et al. 2001 with permission of *Oecologia Montana*)

Species	temporal variability (n=14)			Spatial variability (n=80)		
	mean	std	CV,%	mean	std	CV,%
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

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 variation in temporal shoot density. A low rate of temporal variation was observed for *Carex curvula* in the Alps (Erschbamer et al. 1998).

Our results support the idea that the dynamics and spatial structure of plant communities may be interrelated. The behaviour of SBC species was more consistent with the competitive hierarchy model of Lehman & Tilman (1998) 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).

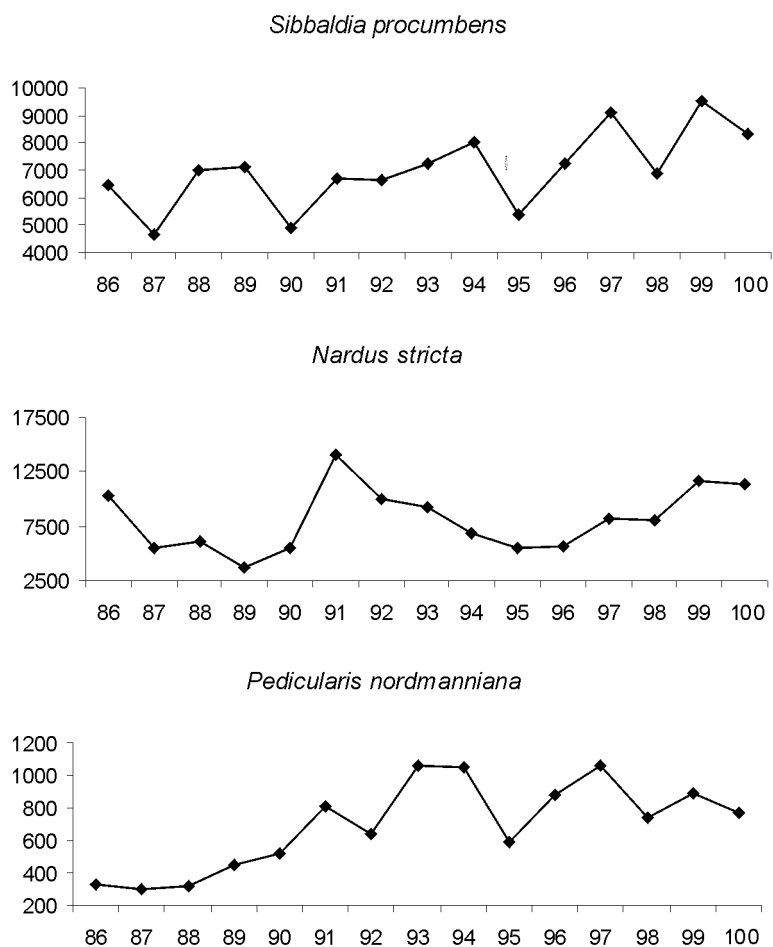


Figure 5.33. Examples of dynamics of 3 alpine species from SBC. Abscissa - years of observation (1900+), ordinate - total number of shoots on permanent plots (5 m²) (from Zakharov et al. 2001).

5.6.4. Species groups according to their dynamic behaviour and weather conditions

Analysis of the correlation matrix allowed as to distinguish groups of species with similar dynamic behaviour (Onipchenko et al. 2001). Several small correlated groups were obtained in ALH (Fig. 5.34). *Eritrichium caucasicum*, *Gentiana pyrenaica*, *Agrostis vinealis*, and *Luzula spicata*

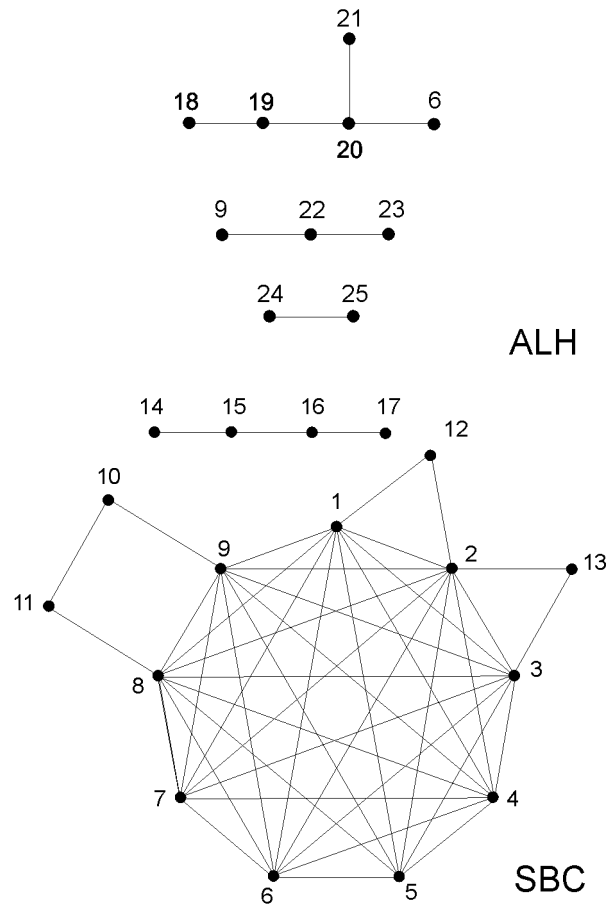


Figure 5.34. Correlation diagrams for groups of species with similar dynamic behaviour. Values of positive Spearman correlation coefficient (significance level $p < 0.01$) are indicated by solid lines within communities only. Communities: ALH - alpine lichen heath, SBC - snow bed community. Species: 1 - *Carum meifolium*, 2 - *Pedicularis nordmanniana*, 3 - *Luzula multiflora*, 4 - *Anthoxanthum odoratum*, 5 - *Corydalis conorrhiza*, 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 alpinus*, 24 - *Arenaria lychnidea*, 25 - *Carum caucasicum*. (from Onipchenko et al. 2001 with permission of *Oecologia Montana*)

formed the largest group at a significance of $p = 0.01$. *Festuca ovina*, *Minuartia circassica* and *Erigeron alpinus* formed another group, while *Carum caucasicum* and *Arenaria lychnidea* were positively correlated with each other. But between groups there were many positive correlations for the species at a lower level of significance ($0.05 > p > 0.01$), thus the species of those three groups did not show major differences in dynamics. Completely different shoot dynamics was shown by *Trifolium polyphyllum*. This species had negative correlations ($p < 0.05$) with 3 species of the second group (*Minuartia circassica*, *Festuca ovina*, *Erigeron alpinus*).

A completely different picture was obtained for SBC where most of the species showed positive correlations with each other (Fig. 5.34). 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 the Spearman correlation coefficients 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.

A few significant correlation coefficients were obtained between shoot numbers and current or previous weather conditions (Table 5.22.). Several SBC species (*Anthoxanthum odoratum*, *Luzula multiflora*, *Phleum alpinum*) showed a 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 the number of generative shoots of *Anemone speciosa*. Generative shoots of *Eritrichium caucasicum* correlated negatively with precipitation in April of the current year.

5.6.5. Trends in species dynamics

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

Table 5.22. Significant Spearman correlation coefficients (CC, $p < 0.001$) 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 (from Onipchenko et al. 2001 with permission of *Oecologia Montana*)

Species	Com	Sh	Weather parameter	CC
<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

dominants alternate according to climatic variations between years; 3) “demutations” - cycles include 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.

Several species of ALH and SBC showed a significant linear trend for the period of observation (Onipchenko et al. 2001). A positive trend (significant increase of shoot number) was found for 8 species in SBC (*Anthoxanthum odoratum*, *Carum meifolium*, *Corydalis conorhiza*, *Festuca brunnescens*, *Festuca ovina*, *Gentiana pyrenaica*, *Hyalopoa pontica*, *Luzula multiflora*), 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 (Onipchenko et al. 2001). Far less (5 from 19 studied species, *Arenaria lychnidea*, *Campanula tridentata*, *Erigeron alpinus*, *Festuca ovina*, *Minuartia circassica*) ALH species showed an increase in shoot numbers. Only one species (*Trifolium polyphyllum*) showed a decrease in population density in ALH.

As a whole, 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 2002). 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 abundance in meadow species may therefore be the result of secondary succession after the ending of grazing.

Other possible explanations of the successional trends may be connected with current climate change. We have found a positive trend for minimal October temperature for the Teberda meteorological station during the last 19 years (Blinkova & Onipchenko 2001). But only few species demonstrated a positive correlation with the October temperature (Table 5.22). The lists of the species with such correlations and linear trends overlap only slightly.

Most of the SBC species that had a concordant dynamic behaviour (Fig 5.34.) 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 the 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 (centuries and millennia) (Pavlova & Onipchenko 1992, Blinnikov 1994).

5.6.6. Autocorrelation analysis

According to their autocorrelograms 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 a lag of 1 year. That is, next year's number of shoots depended on the current year's shoot density. Nine species (3 from ALH and 6 from SBC) belonged to this group (Table 5.23), suggesting that relatively more species from the snow bed community demonstrated such conservative dynamics.

Table 5.23. Significant autocorrelation coefficients for a lag of 1 year. R - correlation coefficient, *t*-criteria value (n=13)

Species	Community	R	<i>t</i>
<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

So, 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.

5.6.7. ALH revegetation after wild boar digging

5.6.7.1. Species richness

We recorded a total of 20 vascular plant species on the disturbed plots during the whole period of observation. The number of species recorded annually increased from 10 in 1981 to 16 in 1994, as well as the average number per plot (from 5.2 to 10.2, respectively). The t-test shows that the difference between the disturbed and control plots is statistically significant at the 1% level in the two first years and at the 5% level in the following four. By year 10 the average number of vascular plant species on the disturbed plots was approximately the same as on the control (about 9.5 species per plot) one (Fig. 5.35). Floristic richness per plot increased due to the gradually increasing frequency of species registered from the very beginning of our observation (*Luzula spicata*, *Carum caucasicum*) as well as the arrival of new species (*Eritrichium caucasicum*, *Veronica gentianoides*, *Euphrasia ossica*, *Pedicularis comosa*, *Alchemilla caucasica*). All of the recorded species are typical of alpine lichen heaths. There appeared no species alien to this type of community. This proves the statement that the species composition of plant communities in the high altitude areas does not change during revegetation successions (McMahon 1982). Severe environmental conditions prevent diaspores of other species from invading disturbed plots.

5.6.7.2. Plant cover

Overall the revegetation of alpine lichen heath has been proceeding slowly: the traces of digging are clearly distinguishable even 15 years after the disturbance had happened. The bare soil area has reduced considerably (from 71% to 5% on average) during the time of our observation, whereas the cover of vascular plants has increased from 2% to 32%, getting close to the control one. At the same time the cover of fruticose lichens has reached only 27%. It makes up approximately half of the control value. The cover of bryophytes on the disturbed plots has exceeded a few times the control one that was never more than 1% (Fig. 5.36). In all probability it is connected with the sudden denudation of a considerable piece of soil surface after wild boar disturbance. It is supposed that bryophyte species (particularly *Polytrichum juniperinum* and *Pohlia nutans*) demonstrate the ability for quick colonisation of bare soil areas.

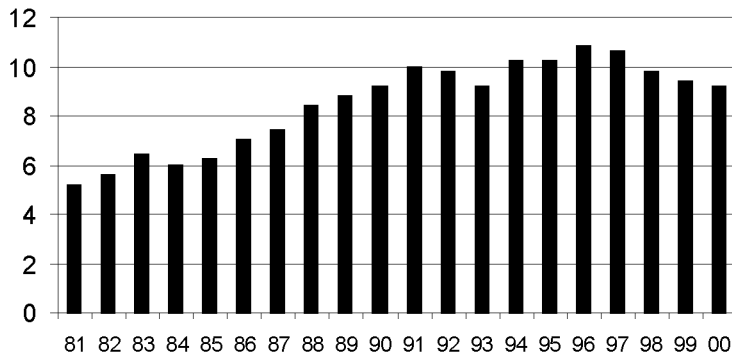


Figure 5.35. Dynamics of floristic richness on wild boar diggings in alpine lichen heath. Abscissa - years of observation (1900+), ordinate - mean number of vascular plant species in a plot of 25 x 25 cm

Thus, there is a marked difference between the components of alpine lichen heath in the rate of recovery. The slowest to recover are fruticose lichens. Apparently this is due to the low rate of their growth, especially of *Cetraria islandica*, *Cladonia mitis* and *Thamnolia vermicularis*. On the other hand, because of frequent strong winds, fruticose lichens cannot develop in the alpine lichen heaths without the "framework" of the community, formed by vascular plants whose floristic composition does not change significantly after removal of lichens (Chapter 5.3, Onipchenko 1985, 1994b). It is interesting that the investigation of a New Zealand high-alpine cushion field has yielded similar results: 11 years after mechanical disturbance the lichen cover dominated by *Cetraria islandica*, *Thamnolia vermicularis* and *Alectoria nigricans* had not recovered (Roxburgh et al. 1988).

5.6.7.3. Shoot density

In the first year of our observation the shoot density of most species on the disturbed plots was significantly lower than that of the control (Onipchenko & Golikov 1996, Fig. 5.37). In later years a drastic increase was observed for some graminoids - *Festuca ovina*, *Luzula spicata*, *Carex* spp. (*C. umbrosa*, *C. sempervirens*) - due to the intensive vegetative growth of the plants remaining after the disturbance. It is suggested that these species demonstrate the "explerent" strategy properties sensu Ramenskii (1938), namely a quick clonal growth and colonisation ability (Chapter 6.3)

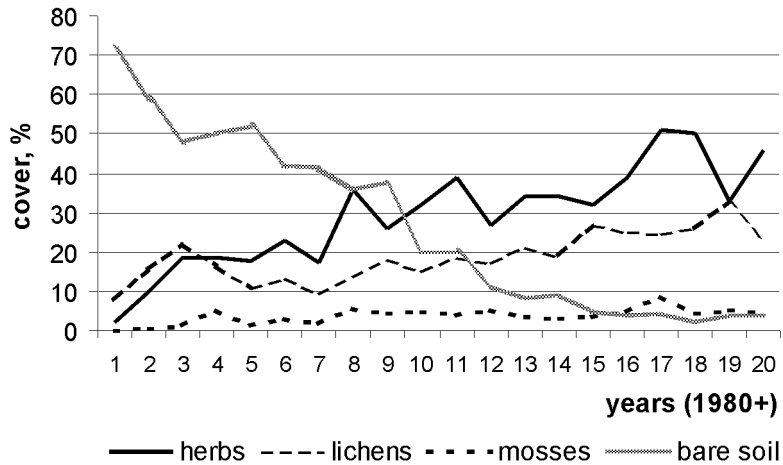


Figure 5.36. Dynamics of plant and bare soil cover after boar digging

There are some observations (Shiffers 1953, Tsareva 1978, Brown & Johnston 1979) that *Luzula spicata* is one of the first plants to occupy the disturbed sites in high altitude areas. It is therefore recommended for the restoration of alpine communities.

Seed reproduction is the main factor promoting the restoration of taprooted polycarpics, such as *Carum caucasicum* and *Campanula tridentata*. Their seedlings have appeared on the dug plots in the following fashion: 1) from the soil seed bank (Semenova and Onipchenko 1994); 2) from the adult individuals remaining on site after disturbance; 3) from the nearest surroundings. That is why in the population structure of these species on the disturbed plots juveniles are significantly more than on the control plots. On the other hand, the proportion of generative plants is considerably less than in the control.

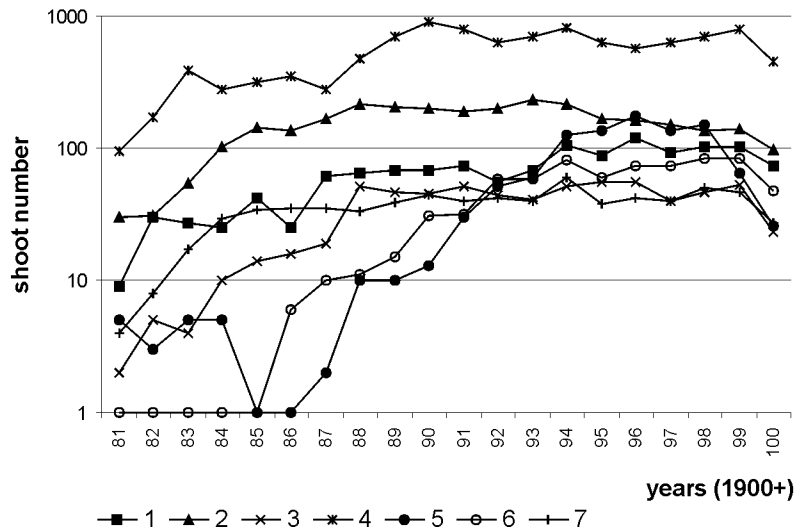


Figure 5.37. Shoot number dynamics for 7 abundant species after boar digging. Species: 1 – *Campanula tridentata*, 2 - *Carex umbrosa*, 3 - *Carum caucasicum*, 4 - *Festuca ovina*, 5 - *Gentiana pyrenaica*, 6 - *Helictotrichon versicolor*, 7 - *Luzula spicata*

The shoot density of *Anemone speciosa* has been recovering very slowly. Apparently, small seed yield capacity and the lack of vegetative reproduction of this species can explain this fact. The same holds true for *Eritrichium caucasicum*.

We can conclude that the species composition does not change considerably during local revegetation in the alpine zone. The most abundant species of alpine lichen heath remained dominants on the disturbed plots. Disturbance changes only the relative role of some groups of species. We proposed a number of characteristic features to distinguish stages of revegetation of alpine lichen heath from the undisturbed communities (at least during several ten-year periods): 1) presence of some patches of bare soil surface; 2) low coverage of fruticose lichens; 3) greater abundance of graminoids; 4) low abundance of *Anemone speciosa*.