

Experimental investigation of alpine plant communities in the Northwestern Caucasus

Autor(en): **Onipchenko, Vladimir G. / Blinnikov, Mikhail S. / Sennov, Andrej V.**

Objekttyp: **Article**

Zeitschrift: **Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübél, in Zürich**

Band (Jahr): **115 (1994)**

PDF erstellt am: **03.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-308979>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

**Experimental Investigation of Alpine Plant Communities
in the Northwestern Caucasus**

Edited by
Vladimir G. ONIPCHENKO and
Mikhail S. BLINNIKOV

1994

CONTENTS

Preface	5
1. Study area and general description of the investigated communities (ONIPCHENKO V.G.)	6
1.1. Site description	6
1.2. Climate	7
1.3. Geology and soils	8
1.4. Plant communities	9
1.4.1. Alpine lichen heaths (ALH)	10
1.4.2. <i>Festuca varia</i> dominated grasslands (FVG)	11
1.4.3. <i>Geranium gymnocaulon</i> - <i>Hedysarum caucasicum</i> meadows (GHM)	16
1.4.4. Snow bed communities (SBC)	16
1.4.5. Other communities	18
Summary	22
2. Phytolith analysis and Holocene dynamics of alpine vegetation (BLINNIKOV M.S.)	23
2.1. Introduction	23
2.2. Methods	25
2.3. Results	31
2.3.1. Principal phytolith forms found in alpine plants and soils	31
2.3.2. Subrecent phytolith assemblages and present vegetation	34
2.3.3. Phytolith frequencies in soil profiles under four alpine communities	36
2.3.4. Distribution of different forms of silica phytoliths in four soil profiles	37
Summary	39
3. Experimental research of alpine communities with use of reciprocal transplantations (SENNOV A.V. and ONIPCHENKO V.G.)	41
3.1. Introduction	41
3.2. Methods	43
3.3. Results and discussion	45
3.3.1. Transplantations of alpine lichen heaths (ALH)	45
3.3.2. Transplantations of <i>Festuca varia</i> dominated grasslands (FVG)	50
3.3.3. Transplantations of <i>Geranium gymnocaulon</i> - <i>Hedysarum caucasicum</i> dominated meadows (GHM)	51
3.3.4. Transplantations of snow bed communities (SBC)	54
3.3.5. Morphological changes of separate species	59
Summary	60
4. "Mass-effect" in alpine communities of the Northwestern Caucasus (ONIPCHENKO V.G. and POKARZHEVSKAYA G.A.)	61
4.1. Introduction	61
4.2. Methods	62
4.2.1. Field methods	62
4.2.2. Analysis data	62
4.3. Results	63
4.3.1. Floristic richness	63
4.3.2. Degree of heterogeneity	64
4.3.3. Dependence on orientation along slope	65
4.3.4. Distribution among frequency classes	66

4.3.5	Results of Euclid distance calculating	66
4.4	Discussion	67
	Summary	68
5.	Soil seed banks	69
	(SEMENOVA G.V. and ONIPCHENKO V.G.)	
5.1	Introduction	69
5.2.	Materials and methods	69
5.3	Results and discussion	71
5.3.1	Size of alpine seed banks	71
5.3.2	Seed bank composition	73
5.3.3	Species diversity	76
5.3.4	Spatial distribution of buried seeds	78
5.3.5	Dynamics of seed germination	79
	Summary	82
6.	Natural "gaps" in alpine meadows and plant population strategies	83
	(ONIPCHENKO V.G. and RABOTNOVA M.V.)	
6.1	Introduction	83
6.2	Materials and methods	83
6.3	Results and discussion	86
	Summary	88
7.	Shading experiments in the alpine grasslands	89
	(ONIPCHENKO V.G., BLINNIKOV M.S. and SEMENOVA G.V.)	
7.1	Introduction	89
7.2	Methods	89
7.3	Results and discussion	91
7.3.1	Changes on plots shaded for most of the vegetative season (all-summer variant)	91
7.3.2	Changes on plots shaded for the first half of the vegetative season	97
7.3.3	Changes on plots shaded for the second half of the vegetative season	97
7.3.4	Changes in floristic diversity of ALH and FVG under shading	98
	Summary	99
8.	The spatial structure of the alpine lichen heaths (ALH): hypothesis and experiments	100
	(ONIPCHENKO V.G.)	
8.1	Introduction	100
8.2	Methods	103
8.2.1	Lichen removal experiments	103
8.2.2	Fertilization experiments	103
8.2.3	Root cutting experiments	104
8.3	Results and discussion	104
8.3.1	Lichen removal experiments	104
8.3.2	Fertilization experiments	105
8.3.3	Root cutting experiments	110
	Summary	111
	References	112
	Addresses of the authors	118

PREFACE

Alpine communities have drawn the close attention of many plant ecologists in recent decades. These scenic and comparatively undisturbed habitats can serve as a convenient object for long-term ecological research. Unfortunately, there have been few detailed investigations of structure and processes in alpine communities, especially in the Caucasus.

Therefore, a long-term ecological research field station was founded by a group of scientists from Moscow State University in the alpine zone of Teberda State Reserve in 1977. The station was established to study the composition, structure and dynamics of typical alpine ecosystems of humid mountains in the Northwestern Caucasus. The other goal was to study mechanisms of species coexistence and to test fitness of some recent ecological ideas in field experiments.

The present volume contains some recent experimental data both on population ecology of alpine plants and phytosociology of alpine communities. The first five chapters consider the results of comparative study of several alpine communities. The other three describe experiments in particular phytocoenoses.

The authors wish to continue their research in the future. Any critical comments would be greatly appreciated.

We express our sincere gratitude to our teachers, Professors Tikhon A. Rabotnov, Leonora A. Grishina and Vadim N. Pavlov for their constant attention and support of our work. Thanks are also due to all members of the Moscow University expedition for their help in gathering field materials, and to the administration and staff of Teberda State Reserve for their continual assistance in the organization of field research. We wish to thank Mrs. Allison Smith for her helpful comments on the earlier draft of this volume. We are particularly thankful to Prof. Elias Landolt, who invited us to undertake this book. We would like to thank Mrs. Susy Dreyer for all her efforts in preparing this volume.

Our work was supported by "The Russian Universities" government grant.

Moscow

V. G. Onipchenko
M. S. Blinnikov

1. Study area and general description of the investigated communities

Vladimir G. ONIPCHENKO

Acknowledgement

I would like to thank O. Jurtzeva for preparing the figures, E. Ignatova and M. Ignatov for determining the moss samples, M. Makarov for helpful comments on soil description, and M. Blinnikov for his help with the English text.

1.1. SITE DESCRIPTION

The study site is located in Teberda State Reserve, a part of the Karatchaev-Cherkessian Republic in the Northwestern Caucasus. It is situated on Mount Malaja Hatipara, at 2650-2800 m a.s.l. ($43^{\circ}27'$ N, $41^{\circ}41'$ E). This mountain belongs to the system of small ranges near the Great (Bolshoj) Caucasus Range, which is only about 22 km from our study area (Fig. 1.1).

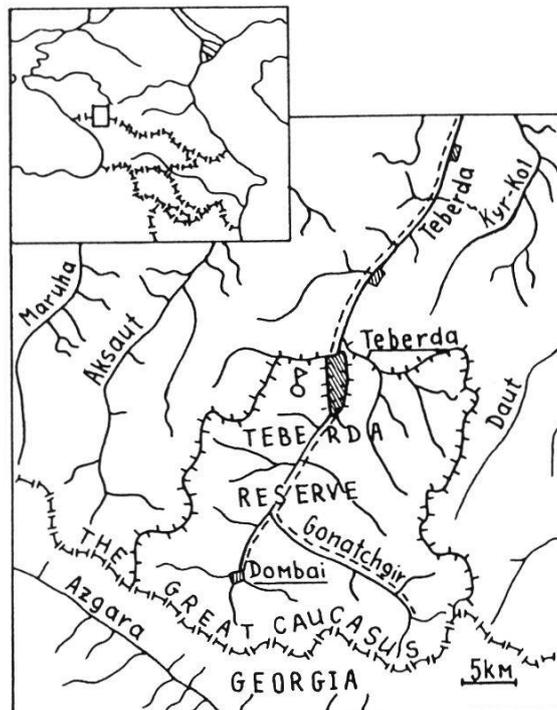


Fig. 1.1. Location of the study site.

The study area is situated in the typical alpine zone, as though climatic timberline should lie at 2400-2500 m a.s.l., but the actual timberline does not run higher than 2350 m. a.s.l.

1.2. CLIMATE

Using data from the nearest meteorological stations at the reserve ("Meadow - 5", 1 km to the south, 2750 m a.s.l. and "Teberda," 5 km to the east, 1328 m a.s.l., GRISHINA et al. 1986) we drew a climatic diagram for the study area (Fig. 1.2). The climate of the alpine zone can be considered as the mountain climate of the temporal zone type X(VI), according to WALTER et al. (1975). Mean annual temperature is about -1.2°C , and mean precipitation 1406 mm. These features are similar to those of some areas in the Swiss Alps, i.e. Weissfluhjoch (2667 m a.s.l.) near Davos (ZINGG 1961). Air humidity averages about 79% during summer months. Average duration of time with 100% air humidity is about four hours per day. Insolation at the soil level is about two times less than potential because of the clouds (see GRISHINA et al. 1986). The warmest month is August with a mean temperature of $+8.3^{\circ}\text{C}$, but frost can occur throughout the summer.

South winds predominate in the area, so the south slopes are windward and north slopes are leeward with heavy snow accumulation (snow beds), determining the pattern of vegetation cover (see below).

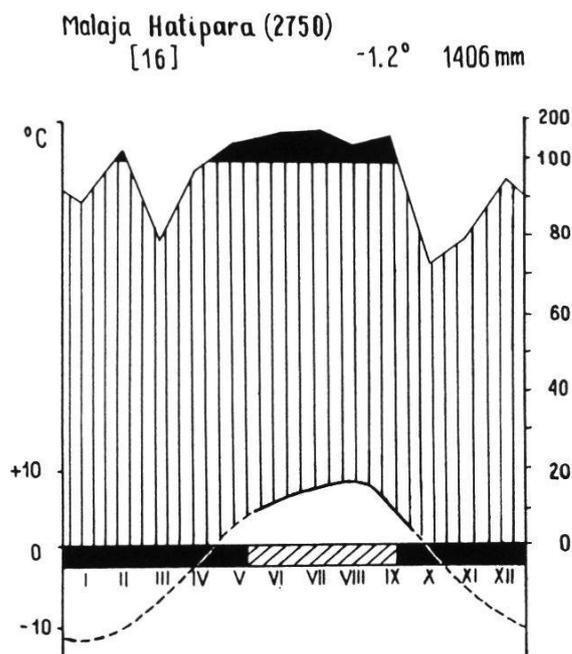


Fig. 1.2. Climatic diagram of meteorological station "Meadow - 5" on Mt. M. Hatipara.

1.3. GEOLOGY AND SOILS

Siliceous rock materials prevail in the Teberda Reserve. Biotic schists and granites are the main rock types in the study area. Biotic, quartz and feldspars (acid plagioclases and microcline) are the most important primary minerals in the soils (GRISHINA and MAKAROV 1987 in RABOTNOV 1987a). Alpine mountain meadow soil, according to the Soviet soil classification of 1977, is the most wide-spread soil type in the alpine zone of the area. The soils are shallow with a well developed turf horizon and are characterized by a high stony content, an acid or strong acid reaction, a great humus accumulation in upper horizons, and a low rate of base saturation. There are no signs of podsolization in the soils. Only a slight rate of gleization can be observed in the soils of snow beds with water saturation during the somewhat short thaw period. Thus, alpine soils of the area differ considerably from podzolic and pseudogley soils of the Alps (BOUMA et al. 1969, BOUMA and VAN DER PLAS 1971, GRACANIN 1972, POSCH 1977, NESTROY 1984, MÜLLER 1987), but they are similar to alpine turf soils of the Rocky mountains (Colorado) (RETZER 1956, 1974, JOHNSON and CLINE 1965) and to the alpine humus soils in Australia (COSTIN et al. 1952, COSTIN 1955). According to the USA soil classification, they belong to Cryorthents (Orthents, Entisols) (Supplement... 1967). The soils have a high water permeability (Table 1.1). The highest permeability (about 5 mm/min.) was observed in the soils of *Geranium-Hedysarum* meadows, which may be connected with the significant burrowing activity of voles in this community (see below).

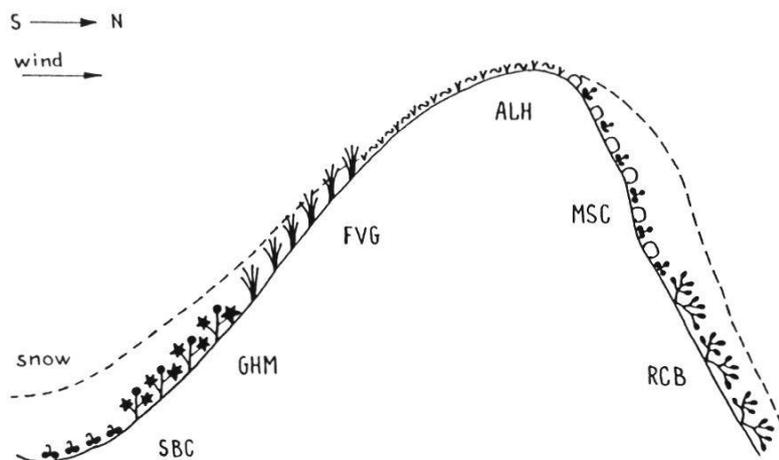


Fig. 1.3. Distribution of investigated communities over mesorelief forms. ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities, MSC = communities on moist screes, RCB = *Rhododendron caucasicum* bush communities.

Table 1.1. Several soil properties of the studied area (from GRISHINA et al. 1993). ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = Snow bed communities.

Community	ALH	FVG	GHM	SBC
Depth of soil humus layers, cm (Ad+A1+AB)	15-20	20-24	19-22	16-17
pH of soil upper layer (water extract)	5.6	5.1	5.1	4.7
pH of soil upper layer (KCl - extract)	4.0	4.0	4.1	3.8
Stones content in layer 0-10 cm (volume %)	13	10	9	5
Loss on ignition in layer 0-10 cm (%)	18	23	22	29
Total nitrogen in the upper soil layer (%)	0.77	0.73	0.56	1.32
Humus stock in the layer 0-40 cm, kg/m ²	15.6	19.6	23.0	32.5
Water filtration coefficient for soils, mm/min	1.1	3.7	5.4	1.9
Available nutrients in the upper soil layer, mg/100 g				
N(NH ₄)	1.2	3.2	4.2	6.1
P	0.6	0.5	0.8	0.7
K	29	19	31	61

The studied communities occupy different position in the mesorelief and the soils can be considered as catena (Fig. 1.3). The stone content decreases, while the fine grained soil fraction, actual and hydrolytic soil acidity, content of exchangeable ammonium and storage of organic matter increase from upper parts of the slopes to snow bed depressions (Table 1.1, GRISHINA et al. 1993). The soils are poor in available nitrogen, phosphorus and calcium, but rich in potassium due to parent rock material. It seems that the comparatively high ammonium content in the soils of meadow and snow bed communities is caused by a disturbance regime (TILMAN 1988) and, correspondingly, a short vegetative season which prevent the full uptake of ammonium by the plants.

1.4. PLANT COMMUNITIES

The main objects of our investigation were four types of alpine plant communities (their abbreviations are shown in parentheses): 1) Alpine lichen heaths (ALH), 2) *Festuca varia* dominated grasslands (FVG), 3) *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM), 4) Snow bed communities (SBC).

They occupy different positions in the mesorelief and can be considered as one catena (toposequence) (Fig. 1.3, Table 1.2). Two sample areas for each community type are used. One sample area was drier with a lower snow accumulation ("U" or "upper"), the other, damper with a higher accumulation of

Table 1.2. General characteristics of sample areas of the communities. (* from FOMIN et al. 1989).

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

Community type	ALH	FVG	GHM	SBC
Occupied relief forms	crests, ridges, windward slopes	slopes (often steep)	leeward slopes, small depressions	bottom of kars, deep depressions
Depth of snow cover in winter (m)	0-0.3	0.5-1.5	1.5-3	4 and more
Duration of vegetative season (months)	4.5-5.5	3.5-4.5	2.5-3.5	2-2.5
Exposition	S	SSW	SW	SW
Steepness (°)	15	10	5	1
Number of vole burrows/ha (average and s.e.)*	300+110	1500+290	3700+590	30+30

snow ("L" or "lower"). So all investigated sample areas can be presented in the following sequence from snow free to snow bed communities:

ALH(U)-ALH(L)-FVG(U)-FVG(L)-GHM(U)-GHM(L)-SBC(U)-SBC(L).

These communities are most wide-spread closed alpine communities in the study area. Some of our observations dealt with *Rhododendron caucasicum* bush communities (RCB), high mountain bogs and open plant communities on screes.

1.4.1. Alpine lichen heaths (ALH)

ALHs occupy windward crests and slopes with very thin (up to 10-15 cm) or no snow cover in the winter. So deep freezing is typical for the soils there. The vegetative season lasts about five months (from May to September). Fruticose lichens are the main dominants (mostly *Cetraria islandica*) (Table 1.4).

These communities are rather rich in vascular plant species, especially on small plots (Table 1.3, ONIPCHENKO and SEMENOVA 1988). According to their floristic composition the following syntaxonomic position of the communities are suggested (ONIPCHENKO et al. 1987):

Juncetea trifidi Hadač 1944

Caricetalia curvulae Br.-Bl. 1926

Anemonion speciosae Minaeva 1987

Pediculari chroorrhynchae-Eritrichietum caucasici Minaeva 1987

P.c.-E.c. oxytropidetosum kubanensis Minaeva 1987.

Table 1.3. Floristic diversity of the investigated communities (average number of vascular plant species for different plot size, from ONIPCHENKO and SEMENOVA 1988).

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* -*Hedysarum caucasicum* meadows, SBC = snow bed communities, DSC = communities on dry screes.

Community	Side of square plots (cm)							
	5	10	25	50	100	200	500	1000
DSC	1.9	4.5	11.2	16.8	22.1	33.6	40.2	46.0
ALH	2.9	6.2	14.8	20.2	25.0	30.6	36.0	39.8
FVG	2.5	4.6	11.1	17.8	24.4	40.4	48.6	56.8
GHM	2.3	5.3	11.4	15.8	19.5	26.4	30.6	35.0
SBC	3.3	5.1	7.9	9.4	11.3	14.8	18.0	-

Cetraria islandica is an absolute dominant among lichens with about 330 g/m² biomass (all values represent dry mass). The total lichen biomass is about 440 g/m² (ONIPCHENKO 1983, 1985). Above-ground vascular plant biomass was estimated at 110 g/m², below-ground 480 g/m² and corresponding values for mortmass were 230 and 403 g/m². More detailed characteristics of the phytomass are presented in several papers (ONIPCHENKO 1983, 1985, 1990). *Anemone speciosa*, *Antennaria dioica*, *Campanula biebersteiniana*, *Carex sempervirens*, *Carex umbrosa* and *Festuca ovina* representing more than 5% of above-ground biomass can be considered dominants among vascular plants.

ALHs have a very specific space structure, which is discussed in chapter 8 of this volume.

1.4.2. *Festuca varia* dominated grasslands (FVG)

FVGs are firm-bunch grass communities (Table 1.5). They occupy slopes with little snow accumulation (about 0.5-1 m). Snow cover lies until the second half of May or the first half of June, so the vegetative season lasts about four months.

Apparently, the syntaxonomic position of these communities is following:

Nardo-Callunetea Prsg. 1949

Nardetalia Prsg. 1949

Festucion variae Br.-Bl. 1925

Violo oreadis-Festucetum variae Rabotnova 1987 in ONIPCHENKO et al. 1987.

Table 1.4. Floristic composition of alpine lichen heaths and communities on dry screes. ALH = alpine lichen heaths (U = upper, L = lower sample areas), DSC = community on dry screes, K1 = Raunkiaer's frequency classes in *P.c.-E.c. oxytropidetosum kubanensis* and *P.c.-E.c. chamaesciadietosum acaule* correspondingly. Abundance values are given according to Braun-Blanquet scale. (* see Table 1.7)

Communities Sample area	AHL		DSC		
	U	L	K1	K1	
Cover of vascular plants (%)	30	40		35	
Cover of bryophytes (%)	<1	<1		<1	
Cover of lichens (%)	50	40		5	
Vascular plants					
<i>Aetheopappus caucasicus</i> Sosn.	.	.	-	1	IV
<i>Alchemilla caucasica</i> Buser	1	+	V	.	IV
<i>Anemone speciosa</i> Adam ex G.Pritz	2	2	V	1	V
<i>Antennaria dioica</i> (L.) Gaertn.	1	1	V	1	III
<i>Anthemis iberica</i> Bieb.	.	r	I	+	I
<i>Anthemis sosnovskyana</i> Fed.	.	.	-	1	V
<i>Anthyllis vulneraria</i> L.*	.	.	-	1	V
<i>Arenaria lychnidea</i> Bieb.	+	+	V	+	V
<i>Asperula cristata</i> (Somm.et Levier) V.Krecz.	.	.	-	+	I
<i>Aster alpinus</i> L.	+	+	IV	1	IV
<i>Astragalus levieri</i> Freyn ex Somm. et Levier	.	.	-	+	I
<i>Bromopsis variegata</i> (Bieb.) Holub	.	.	-	1	IV
<i>Campanula biebersteiniana</i> Schult.	2	2	V	.	IV
<i>Campanula ciliata</i> Stev.	.	.	-	+	IV
<i>Campanula collina</i> Bieb.	.	1	V	1	V
<i>Campanula saxifraga</i> Bieb.	.	.	-	+	III
<i>Carex sempervirens</i> Vill.*	1	1	V	1	IV
<i>Carex umbrosa</i> Host	1	1	V	1	II
<i>Carum caucasicum</i> (Bieb.) Boiss.	1	1	V	+	III
<i>Chamaescadium acaule</i> (Bieb.) Boiss.	.	.	-	+	V
<i>Deschampsia flexuosa</i> (L.) Trin.	.	.	-	+	-
<i>Draba siliquosa</i> Bieb.	.	.	-	+	-
<i>Empetrum nigrum</i> L.	.	.	-	+	-
<i>Erigeron uniflorus</i> L.	1	+	IV	+	IV
<i>Eritrichium caucasicum</i> (Albov) Grossh.	+	+	V	+	IV
<i>Euphrasia ossica</i> Juz.	r	+	IV	+	IV
<i>Festuca ovina</i> L.	1	2	V	1	V
<i>Festuca varia</i> Haenke	.	.	-	+	I
<i>Fritillaria lutea</i> Mill.	+	+	V	.	-
<i>Galium verum</i> L.	.	.	-	+	I
<i>Gentiana aquatica</i> L.	.	r	I	+	II
<i>Gentiana biebersteinii</i> Bunge	.	+	II	+	IV
<i>Gentiana djimilensis</i> C. Koch	1	1	V	+	-
<i>Gentiana oschtenica</i> (Kusn.) Woronow	.	+	II	+	IV
<i>Gentiana septemfida</i> Pall.	+	+	III	.	III
<i>Gnaphalium supinum</i> L.	.	.	-	+	I
<i>Helictotrichon versicolor</i> (Vill.) Pillger*	1	1	V	1	V
<i>Juniperus hemisphaerica</i> J. et C. Presl	.	.	-	+	I

Table 1.4 (continued)

Communities Sample area	AHL			DSC	
	U	L	K1		K1
<i>Lloydia serotina</i> (L.) Reichenb.	.	.	-	+	II
<i>Luzula spicata</i> (L.) DC.	+	+	V	+	IV
<i>Minuartia circassica</i> (Albov) Woronow	+	+	V	1	V
<i>Minuartia recurva</i> (All.) Schinz et Thell.	.	.	-	+	II
<i>Myosotis alpestris</i> F.W. Schmidt	.	.	-	+	III
<i>Oxytropis kubanensis</i> Leskov	1	1	V	1	I
<i>Pedicularis caucasica</i> Bieb.	+	.	I	.	II
<i>Pedicularis chroorrhyncha</i> Vved.	+	+	V	1	V
<i>Plantago saxatilis</i> Bieb.	.	+	V	.	I
<i>Polygonum bistorta</i> L.	+	+	V	1	V
<i>Potentilla gelida</i> C.A. Mey.	+	1	IV	1	III
<i>Potentilla nivea</i> L.	r	.	II	.	II
<i>Primula algida</i> Adam	.	+	IV	+	II
<i>Primula ruprechtii</i> Kusn.	.	r	II	+	II
<i>Pulsatilla albana</i> (Stev.) Bercht. et C. Presl	.	.	-	+	III
<i>Ranunculus oreophilus</i> Bieb.	+	+	V	+	III
<i>Scabiosa caucasica</i> Bieb.	.	r	III	.	-
<i>Scorzonera cana</i> (C.A. Mey.) O. Hoffm.	.	+	II	+	I
<i>Sedum tenellum</i> Bieb.	.	.	-	+	II
<i>Taraxacum porphyranthum</i> Boiss.	1	.	I	.	-
<i>Taraxacum stevenii</i> (Spreng.) DC.	.	r	III	.	-
<i>Thymus nummularius</i> Bieb.	.	.	-	+	IV
<i>Trifolium polyphyllum</i> C.A. Mey.	1	2	V	+	II
<i>Vaccinium vitis-idaea</i> L.	+	+	V	2	III
<i>Valeriana alpestris</i> Stev.	.	.	-	+	II
<i>Veronica gentianoides</i> Vahl	+	1	V	1	V
Bryophytes					
<i>Desmatodon latifolius</i> (Hedw.) Brid.	+	+	I	.	-
<i>Polytrichum juniperinum</i> Hedw.	+	+	I	+	-
<i>Polytrichum piliferum</i> Hedw.	+	.	I	+	I
<i>Rhytidium rugosum</i> (Hedw.) Kindb.	+	+	V	.	-
Lichens					
<i>Alectoria bicolor</i> (Ehrh.) Nyl.	r	.	I	.	-
<i>Cetraria cucullata</i> (Bellardi) Ach.	1	+	III	+	IV
<i>Cetraria islandica</i> (L.) Ach.	3	2	V	1	V
<i>Cetraria nivalis</i> (L.) Ach.	1	1	V	+	V
<i>Cladonia furcata</i> (Huds.) Schrad.	+	+	II	.	I
<i>Cladonia gracilis</i> (L.) Willd.	+	+	V	.	III
<i>Cladonia mitis</i> (Sandst.) Hale et W. Culb.	2	1	V	.	II
<i>Cladonia pyxidata</i> (L.) Hoffm.	1	1	V	1	V
<i>Cornicularia divergens</i> Ach.	r	.	I	.	-
<i>Dufourea madreporiformis</i> (Wulf.) Ach.	.	.	-	+	IV
<i>Parmelia stenophylla</i> (Ach.) Heug.	.	.	-	+	II
<i>Peltigera rufescens</i> (Weiss) Humb.	+	+	1	-	-
<i>Thamnolia vermicularis</i> (Sw.) Ach. ex Schaer	2	1	V	+	IV

Table 1.5. Floristic composition of alpine grasslands and meadows.

FVG = *Festuca varia* grasslands (U = upper and L = lower sample area), GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, K1 = Raunkiaer's frequency classes in *Viola oreadis*-*Festucetum variae* and *Hedysaro caucasicae*-*Geranietum gymnocauli*, correspondingly. Abundance values according to the Braun-Blanquet scale.

* see Table 1.7.

Communities Sample area	FVG			GHM		
	U	L	K1	U	L	K1
Cover of vascular plants (%)	55	60		75	75	
Cover of bryophytes (%)	<1	-		<1	<1	
Cover of lichens (%)	5	2		2	5	
Vascular plants						
<i>Agrostis vinealis</i> Schreb.	.	.	-	+	+	I
<i>Ajuga orientalis</i> L.	+	.	II	.	.	-
<i>Alchemilla vulgaris</i> L.	+	1	I	.	.	-
<i>Anemone speciosa</i> Adam ex G.Pritz	+	+	IV	.	.	-
<i>Antennaria dioica</i> (L.) Gaertn.	+	+	V	.	.	-
<i>Anthemis iberica</i> Bieb.	1	+	V	1	1	V
<i>Anthoxanthum odoratum</i> L.	1	1	V	2	1	V
<i>Arenaria lychnidea</i> Bieb.	.	+	III	.	.	-
<i>Calamagrostis arundinacea</i> (L.) Roth	1	.	III	.	.	I
<i>Campanula biebersteiniana</i> Schult.	+	+	IV	+	+	V
<i>Campanula collina</i> Bieb.	1	+	V	.	.	-
<i>Carex atrata</i> L.*	1	1	IV	1	1	IV
<i>Carex umbrosa</i> Host	+	+	V	.	.	-
<i>Carum caucasicum</i> (Bieb.) Boiss.	+	+	IV	.	.	II
<i>Carum meifolium</i> (Bieb.) Boiss.	+	+	II	1	1	IV
<i>Catabrosella variegata</i> (Boiss.) Tzvel.	.	.	-	.	1	II
<i>Cerastium purpurascens</i> Adam	+	+	II	.	.	-
<i>Chaerophyllum millefolium</i> DC.	.	+	I	.	.	I
<i>Cruciata laevipes</i> Opiz	+	+	I	.	.	-
<i>Deschampsia flexuosa</i> (L.) Trin.	1	1	V	1	1	IV
<i>Erigeron venustus</i> Botsch.	1	+	I	1	.	III
<i>Euphrasia ossica</i> Juz.	+	.	II	.	+	III
<i>Festuca brunnescens</i> (Tzvel.) Galushko	2	2	III	2	2	V
<i>Festuca ovina</i> L.	1	1	IV	1	.	I
<i>Festuca varia</i> Haenke	3	3	V	.	1	II
<i>Fritillaria lutea</i> Mill.	+	-	V	.	.	-
<i>Gagea glacialis</i> C. Koch	.	.	-	+	+	I
<i>Galium verum</i> L.	+	1	V	+	-	I
<i>Gentiana djimilensis</i> C.Koch	+	+	V	+	+	III
<i>Gentiana septemfida</i> Pall.	1	.	II	+	.	II
<i>Geranium gymnocaulon</i> DC.	.	+	I	2	3	V
<i>Gnaphalium supinum</i> L.	+	.	I	+	+	IV
<i>Hedysarum caucasicum</i> Bieb.	.	1	II	2	1	V
<i>Helictotrichon versicolor</i> (Vill.) Pillger	.	.	II	.	.	-
<i>Hieracium macrolepis</i> Boiss.	1	+	IV	+	.	I
<i>Hyalopoa pontica</i> (Bal.) Tzvel.	.	.	-	.	.	I
<i>Leontodon hispidus</i> L.	1	1	V	1	1	V
<i>Luzula multiflora</i> (Retz.) Lej.*	.	+	I	+	1	V

Table 1.5 (continued)

Communities Sample area	FVG			GHM		
	U	L	K1	U	L	K1
<i>Luzula spicata</i> (L.) DC.	+	.	II	+	.	I
<i>Matricaria caucasica</i> (Willd.) Poir.	+	+	I	1	2	IV
<i>Minuartia aizoides</i> (Boiss.) Bornm.	+	+	IV	1	1	IV
<i>Minuartia circassica</i> (Albov) Woronow	+	+	III	+	.	I
<i>Minuartia recurva</i> (All.) Schinz et Thell.	+	+	IV	+	+	II
<i>Myosotis alpestris</i> F.W.Schmidt	1	+	IV	.	.	-
<i>Nardus stricta</i> L.	2	1	V	2	2	III
<i>Pedicularis chroorrhyncha</i> Vved.	+	+	III	.	.	-
<i>Phleum alpinum</i> L.	.	+	I	.	2	IV
<i>Polygonum bistorta</i> L.	.	1	I	.	.	-
<i>Potentilla aurea</i> L.	.	.	-	.	+	IV
<i>Ranunculus oreophilus</i> Bieb.	+	+	II	+	+	II
<i>Rumex alpestris</i> Jacq.	.	+	I	+	.	II
<i>Scorzonera cana</i> (C.A.Mey.) O.Hoffm.	+	1	V	1	1	II
<i>Sedum tenellum</i> Bieb.	+	.	I	+	+	I
<i>Sempervivum caucasicum</i> Rupr. ex Boiss.	+	.	IV	.	.	-
<i>Senecio aurantiacus</i> (Hoppe ex Willd.) Less.	1	.	II	.	.	-
<i>Senecio kolenatianus</i> C.A.Mey.	+	.	III	.	.	-
<i>Sibbaldia procumbens</i> L.*	+	1	V	1	2	V
<i>Taraxacum confusum</i> Schischk.	+	1	I	.	.	-
<i>Trisetum flavescens</i> (L.) Beauv.	+	.	I	.	+	I
<i>Veronica gentianoides</i> Vahl	1	2	IV	1	1	III
<i>Viola oreades</i> Bieb.	1	+	V	.	.	-
Bryophytes						
<i>Polytrichum juniperinum</i> Hedw.	+	.	III	.	+	II
Lichens						
<i>Cetraria cucullata</i> (Bellardi) Ach.	.	+	I	.	.	-
<i>Cetraria islandica</i> (L.) Ach.	1	1	V	+	1	III
<i>Cladonia mitis</i> (Sandst.) Hale et W.Culb.	1	+	IV	+	.	II
<i>Cladonia pyxidata</i> (L.) Hoffm.	1	+	V	+	1	IV
<i>Stereocaulon alpinum</i> Laurer	1	1	III	.	1	II

These communities have the highest species variety per 10x10 m plots (Table 1.3), but usually only few species can be found on small plots (5x5 cm and 10x10 cm), implying that there must be many comparatively rare species in these communities (Table 1.5, see chapter 4 for Raunkier's histograms).

Festuca varia is an absolute dominant with a biomass of 170 g/m². Only *Nardus stricta* (68 g/m²) can be considered as a codominant in FVG. Total average above-ground vascular plant biomass is about 306 g/m², below-ground biomass 636 g/m². Corresponding values for mortmass are 900 and 565 g/m², which means that FVGs has the highest accumulation of litter.

1.4.3. *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows (GHM)

GHMs occupy the lower parts of slopes and small depressions with a snow cover of 2-3 m. They become snow-free by the end of June or beginning of July, the vegetative season lasting 2.5-3 months.

Geranium gymnocaulon and *Hedysarum caucasicum* are dominants and typical species of this community type (Table 1.5). This community is considered as an association with the following syntaxonomic position:

Nardo-Callunetea Prsg. 1949

Nardetalia Prsg. 1949

Nardion Br.-Bl. 1926

Hedysaro caucasicae-Geranium gymnocauli Rabotnova 1987 in ONIPCHENKO et al. 1987.

GHMs have the highest annual production of the investigated communities (about 550 g/m²). Above-ground vascular plant biomass is 318 g/m², below-ground 1392 g/m² (ONIPCHENKO 1990). *Geranium gymnocaulon*, *Festuca brunnescens*, *Hedysarum caucasicum*, *Nardus stricta*, *Phleum alpinum* and *Anthoxanthum odoratum* are dominants of the GHM. These communities have high rates of soil respiration, nitrogen fixation and denitrification (STEPANOV and ONIPCHENKO 1989). The population density of *Pitymys (Microtus) majori* Thomas (*Glires, Microtinae*) can reach 940 animals/ha during a "peak-year" in these communities (FOMIN et al. 1989). The animals can consume approximately 15% of the annual net production and dig up to 14300 holes/ha in such years (Table 1.2). So severe disturbances are typical for GHMs due to the burrowing activity of the voles.

The variety of plant species is comparatively low in GHMs (Table 1.4). Lichens and mosses play a very small role in these communities (Table 1.5).

1.4.4. Snow bed communities (SBC)

SBCs occupy depressions and floors of kars with heavy snow accumulation (4 m and more). So they have a short 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 (Table 1.6). In some plots *Sibbaldia procumbens* is an absolute dominant. The height of most plants is only 2-3 cm.

Table 1.6. Floristic composition of snow bed communities and communities on moist screes.

SBC = snow bed communities (U = upper and L = lower sample area), MSC = community on moist screes, K1 = Raunkiaer's frequency classes in *Hyalopoa ponticae*-*Pedicularietum nordmanniana* and *Saxifragetum sibiricae*, correspondingly. Abundance values according to the Braun-Blanquet scale. * see Table 1.7.

Communities	SBC		MSC	
	U	L	K1	K1
Sample area				
Cover of vascular plants (%)	95	85		30
Cover of bryophytes (%)	10	10		30
Cover of lichens (%)	<1	2		10
Vascular plants				
<i>Agrostis vinealis</i> Schreb.	+	.	I	.
<i>Alchemilla vulgaris</i> L.	.	.	-	+
<i>Anemone speciosa</i> Adam ex G.Pritz	.	.	I	+
<i>Anthemis iberica</i> Bieb.	.	.	II	1
<i>Anthoxanthum odoratum</i> L.	+	.	II	+
<i>Campanula biebersteiniana</i> Schult.	.	.	IV	+
<i>Campanula collina</i> Bieb.	.	.	-	+
<i>Carex atrata</i> L.*	1	.	V	1
<i>Carex oreophila</i> C.A.Mey.	2	+	I	.
<i>Carex pyrenaica</i> Wahl.*	.	+	IV	+
<i>Carum caucasicum</i> (Bieb.) Boiss.	+	.	V	1
<i>Carum meifolium</i> (Bieb.) Boiss.	+	+	I	.
<i>Catabrosella variegata</i> (Boiss.) Tzvel.	+	+	III	.
<i>Cerastium trigynum</i> Vill.	.	.	-	+
<i>Corydalis conorrhiza</i> Ledeb.	.	+	I	.
<i>Deschampsia flexuosa</i> (L.) Trin.	1	.	II	.
<i>Festuca brunnescens</i> (Tzvel.) Galushko	+	.	I	.
<i>Gagea glacialis</i> C.Koch	+	.	I	.
<i>Gentiana djimilensis</i> C.Koch	+	.	I	.
<i>Gnaphalium supinum</i> L.	2	2	V	+
<i>Hyalopoa pontica</i> (Bal.) Tzvel.	.	+	IV	2
<i>Luzula multiflora</i> (Retz.) Lej.*	.	.	III	1
<i>Matricaria caucasica</i> (Willd.) Poir.	.	.	II	1
<i>Minuartia aizoides</i> (Boiss.) Bormm.	1	1	V	.
<i>Minuartia imbricata</i> (Bieb.) Woronow	.	.	-	1
<i>Nardus stricta</i> L.	2	1	III	.
<i>Pedicularis nordmanniana</i> Bunge	2	1	V	1
<i>Phleum alpinum</i> L.	1	+	I	.
<i>Phryne huetii</i> (Boiss.) O.E.Schulz	.	.	-	+
<i>Potentilla aurea</i> L.	1	1	II	.
<i>Primula meyeri</i> Rupr.	.	.	-	2
<i>Ranunculus oreophilus</i> Bieb.	.	.	-	+
<i>Saxifraga sibirica</i> L.	.	.	-	1
<i>Sedum tenellum</i> Bieb.	.	.	III	1
<i>Senecio taraxacifolius</i> (Bieb.) DC.	.	.	-	1
<i>Sibbaldia procumbens</i> L.*	4	4	V	+
<i>Taraxacum stevenii</i> (Spreng.) DC.	2	2	V	1
<i>Valeriana alpestris</i> Stev.	.	.	-	+

Table 1.6 (continued)

Communities Sample area	SBC			MSC	
	U	L	K1		K1
Bryophytes					
<i>Desmatodon latifolius</i> (Hedw.) Brid.	+	+	I	.	-
<i>Dicranum scoparium</i> Hedw.	.	.	-	1	-
<i>Polytrichastrum alpinum</i> (Hedw.) G.L.Sm.	.	.	-	1	IV
<i>Polytrichum juniperinum</i> Hedw.	1	+	IV	2	I
<i>Polytrichum piliferum</i> Hedw.	2	2	IV	2	I
<i>Sanionia uncinata</i> (Hedw.) Loeske	.	.	I	1	III
Lichens					
<i>Cetraria islandica</i> (L.) Ach.	.	.	I	+	III
<i>Cladonia pyxidata</i> (L.) Hoffm.	+	1	IV	2	IV
<i>Peltigera aphthosa</i> (L.) Willd.	.	.	-	+	I
<i>Stereocaulon alpinum</i> Laurer	.	.	III	+	II

This community type belongs to the class *Salicetea herbaceae*, but *Salix herbacea* and other dwarf willows are absent in the Caucasus. So a new alliance for such vegetation is suggested and the syntaxonomic position of the investigated SBC is the following (ONIPCHENKO et al. 1992):

Salicetea herbaceae Br.-Bl. 1947

Salicetalia herbaceae Br.-Bl. 1926

Sibbaldion Rabotnova 1987

Sibbaldenion Onipchenko 1992

Hyalopoo ponticae-Pedicularietum nordmanniana (RABOTNOVA 1987).

Above-ground vascular plant biomass is about 129 g/m², below-ground 944 g/m². Corresponding values for mortmass are 184 and 592 g/m² (ONIPCHENKO 1990).

1.4.5. Other communities

Comparative observations were also carried out in other alpine communities of the study area: *Rhododendron caucasicum* bush communities (RCB), alpine bogs (BOG) and plant communities on dry and moist screes (DSC and MSC resp.).

Rhododendron caucasicum bush communities develop within the alpine zone mainly on leeward northern steep slopes with significant snow cover. They have a dense *Rhododendron* cover and often a well developed cover of mosses. These communities are comparatively rich in species (Table 1.7).

The syntaxonomic position of the communities is as follows (ONIPCHENKO and SENNOV 1992):

Loiseleurio-Vaccinietea Egger 1952

Empetretalia hermaphroditi Schub. 1960

Rhododendro-Vaccinion Br.-Bl. 1926

Lerchenfeldio-Rhododendretum caucasici Onipchenko et
Sennov 1992

L.-Rh.c. cetrarietosum islandicae Onipchenko et Sennov 1992.

Alpine bogs develop near small streams on valley floors. On Mt. M. Hatipara, two small bogs with a thin layer of peat (ca. 0.5 m) were investigated (Table 1.7). Their syntaxonomic position is as follows (AKATOV 1989):

Scheuchzerio-Caricetea nigrae (Nordhagen 1936) Tx. 1937

Caricetalia nigrae (= *C. fusca*) (Koch 1926) Nordhagen 1936

Caricion davallianae Klika 1934

Primulo auriculatae-Caricetum dacicae Akatov 1989 [*Carex*
dacica Heuff.= *C. nigra* (L.) Reichard ssp. *dacica* (Heuff.) Soo].

Plant communities which have developed on windward dry screes are very similar in floristic composition with ALHs (Table 1.4). DSC and ALH communities are considered to be two subassociations within one association, *Pediculari chroorrhynchae-Eritrichietum caucasici chamaesciadietosum acaule* and *P.c.-E.c. oxytropidetosum kubanensis* Minaeva 1987, resp. DSCs have a high variety of species (Table 1.3), but fruticose lichens play a much smaller role than that in ALHs. DSCs are considered as the successional predecessors of closed ALH communities.

Other communities occupy snow bed screes on leeward slopes and in depressions (MSC) (Table 1.6). This type of community is considered to be positioned within the alliance, *Sibbaldion* Rabotnova 1987, but as a different suballiance (*Saxifragenion sibiricae* Onipchenko 1992) and association *Saxifragetum sibiricae* Onipchenko et Lubeznova 1992 (ONIPCHENKO et al. 1992).

Table 1.7. Floristic composition of *Rhododendron caucasicum* bush communities and alpine bogs.

RCB = *Rhododendron caucasicum* bushes (U = upper and L = lower sample areas), BOG = alpine bogs (sample areas N 1 and 2), K1 = Raunkiaer's frequency classes in *Lerchenfeldio-Rhododendretum caucasicum* and *Primulo auriculatae-Caricetum dacicae* (AKATOV 1989) correspondingly. Abundance values according to the Braun-Blanquet scale.

* These species have the following latin names common in Russian publications:

Anthyllis vulneraria - *A. variegata* Boiss., *Carex atrata* - *C. medwedewii* Leskov, *Carex pyrenaica* - *C. micropodioides* V.Krecz., *Carex sempervirens* - *C. tristis* Bieb., *Helictotrichon versicolor* - *H. adzharicum* (Albov) Grossh., *Luzula multiflora* - *L. pseudosudetica* V.Krecz., *Sibbaldia procumbens* - *S. semiglabra* C.A.Mey.

Communities Sample area	RCB			BOG		
	U	L	K1	1	2	K1
Cover of vascular plants (%)	60	60		50	25	
Cover of bryophytes (%)	40	50		60	80	
Cover of lichens (%)	5	5		-	-	
Vascular plants						
<i>Agrostis vinealis</i> Schreb.	.	+	II	1	+	I
<i>Alchemilla vulgaris</i> L.	.	.	-	2	.	-
<i>Anemone speciosa</i> Adam ex G.Pritz	1	.	III	.	.	-
<i>Anthemis iberica</i> Bieb.	1	+	III	.	.	-
<i>Anthoxanthum odoratum</i> L.	+	1	V	1	1	I
<i>Briza marcowiczii</i> Woronow	.	+	I	2	.	I
<i>Campanula biebersteiniana</i> Schult.	1	.	II	.	.	I
<i>Cardamine uliginosa</i> Bieb.	.	.	-	+	.	III
<i>Carex atrata</i> L.*	.	+	III	.	.	-
<i>Carex nigra</i> L.	.	.	-	2	2	V
<i>Carex pyrenaica</i> Wahl.*	+	.	II	.	.	-
<i>Carum caucasicum</i> (Bieb.) Boiss.	1	1	III	1	1	III
<i>Carum meifolium</i> (Bieb.) Boiss.	.	1	I	.	.	-
<i>Cerastium trigynum</i> Vill.	.	.	-	+	1	II
<i>Cirsium simplex</i> C.A.Mey.	.	.	-	2	.	I
<i>Crepis glabra</i> Boiss.	.	+	I	.	.	-
<i>Deschampsia caespitosa</i> (L.) Beauv.	.	.	-	1	.	I
<i>Deschampsia flexuosa</i> (L.) Trin.	+	2	V	.	.	-
<i>Empetrum nigrum</i> L.	2	1	III	.	.	-
<i>Eriophorum vaginatum</i> L.	.	.	-	.	+	-
<i>Euphrasia ossica</i> Juz.	.	.	I	+	.	-
<i>Festuca ovina</i> L.	+	+	III	.	+	-
<i>Gentiana djimilensis</i> C.Koch	.	.	I	.	+	-
<i>Geranium gymnocaulon</i> DC.	.	1	II	.	.	-
<i>Gnaphalium supinum</i> L.	+	1	III	.	.	-
<i>Hedysarum caucasicum</i> Bieb.	.	1	I	.	.	-
<i>Hieracium macrolepis</i> Boiss.	+	+	III	.	.	-
<i>Huperzia selago</i> (L.) Bernh. ex Schrank et Mart.	+	+	II	.	.	-
<i>Leontodon hispidus</i> L.	.	+	II	.	.	-
<i>Luzula multiflora</i> (Retz.) Lej.*	.	1	II	1	+	I
<i>Minuartia aizoides</i> (Boiss.) Bornm.	+	.	I	.	.	-
<i>Myosotis alpestris</i> F.W.Schmidt	+	+	II	.	.	-
<i>Nardus stricta</i> L.	1	1	III	2	+	II

Table 1.7 (continued)

Communities Sample area	RCB			BOG		
	U	L	K1	1	2	K1
<i>Pedicularis condensata</i> Bieb.	.	+	II	.	.	-
<i>Pedicularis nordmanniana</i> Bunge	+	+	II	1	.	I
<i>Phleum alpinum</i> L.	.	1	I	2	+	II
<i>Polygonum viviparum</i> L.	.	.	-	1	1	-
<i>Potentilla aurea</i> L.	+	.	I	.	.	-
<i>Primula auriculata</i> Lam.	.	.	-	1	.	III
<i>Primula meyeri</i> Rupr.	+	.	II	.	.	-
<i>Pulsatilla aurea</i> (Somm. et Levier) Juz.	.	+	I	.	.	-
<i>Ranunculus oreophilus</i> Bieb.	.	+	II	.	.	-
<i>Rhododendron caucasicum</i> Pall.	3	3	V	.	.	-
<i>Rumex alpestris</i> Jacq.	.	+	II	.	.	-
<i>Saxifraga sibirica</i> L.	.	+	I	.	.	-
<i>Sedum tenellum</i> Bieb.	+	+	III	.	.	-
<i>Senecio taraxacifolius</i> (Bieb.) DC.	1	+	II	.	.	-
<i>Seseli alpinum</i> Bieb.	+	.	II	.	.	-
<i>Sibbaldia procumbens</i> L.*	+	1	IV	2	1	-
<i>Solidago virgaurea</i> L.	+	1	III	.	.	-
<i>Taraxacum officinale</i> Wigg.	+	1	II	.	.	-
<i>Taraxacum stevenii</i> (Spreng.) DC.	.	.	-	+	.	I
<i>Vaccinium myrtillus</i> L.	1	2	V	.	.	-
<i>Vaccinium vitis-idaea</i> L.	+	.	II	.	.	-
<i>Veratrum lobelianum</i> Bernh.	.	+	II	.	.	-
Bryophytes						
<i>Aulaacomnium palustre</i> (Hedw.) Schwaegr.	.	.	-	3	3	-
<i>Brachythecium starkei</i> (Brid.) Schimp. in B.S.G.	+	.	II	.	.	-
<i>Bryum pseudotriquetrum</i> (Hedw.) Gaertn. et al.	.	.	-	1	.	-
<i>Climacium dendroides</i> (Hedw.) Web. et Mohr.	.	.	-	1	.	-
<i>Desmatodon latifolius</i> (Hedw.) Brid.	.	+	I	.	.	-
<i>Dicranum scoparium</i> Hedw.	+	+	V	.	.	-
<i>Hylocomium splendens</i> (Hedw.) Schimp. in B.S.G.	+	.	I	.	.	-
<i>Lophozia sudetica</i> (Nees ex Hueb.) Grolle	.	+	I	.	.	-
<i>Philonotis fontana</i> (Hedw.) Brid.	.	.	-	1	.	-
<i>Plagiothecium denticulatum</i> (Hedw.) Schimp. in B.S.G.	+	.	II	.	.	-
<i>Polytrichastrum alpinum</i> (Hedw.) G.L.Sm.	.	.	I	.	2	-
<i>Polytrichum juniperinum</i> Hedw.	+	+	II	.	.	-
<i>Pseudoleskea incurvata</i> (Hedw.) Loeske	.	+	I	.	.	-
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	+	.	II	.	.	-
<i>Sanionia uncinata</i> (Hedw.) Loeske	+	+	II	1	.	-
<i>Sphagnum capillifolium</i> (Ehrh.) Hedw.	.	.	-	.	2	-
Lichens						
<i>Cetraria islandica</i> (L.) Ach.	2	1	V	.	.	-
<i>Cladonia gracilis</i> (L.) Willd.	+	.	I	.	.	-
<i>Cladonia mitis</i> (Sandst.) Hale et W.Culb.	+	.	III	.	.	-
<i>Cladonia pyxidata</i> (L.) Hoffm.	+	+	V	.	.	-

SUMMARY

The study site is located in Teberda State Reserve in Northwestern Caucasus. It is situated on Mount Malaja Hatipara, at 2650-2800 m a.s.l. (43°27' N, 41° 41' E). Snow accumulation is the main controlling factor for the vegetation pattern of the area. Biotic schists and granites are the main rock types in the study area.

Alpine mountain meadow soil is the most wide-spread soil type in the alpine zone of the area. The soils are shallow with a well developed turf horizon and are characterized by a high stony content, an acid to highly acid reaction, great humus accumulation in the upper horizons, and a low rate of base saturation.

Alpine lichen heaths (ALH), *Festuca varia* dominated grasslands (FVG), *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM) and snow bed communities (SBC) were the main objects of this investigation. Comparative observations were also conducted in *Rhododendron caucasicum* bush communities (RCB), alpine bogs (BOG) and plant communities on dry and moist screes (DSC and MSC resp.). Floristic and syntaxonomic features of the communities are also presented in this work.

2. Phytolith analysis and holocene dynamics of alpine vegetation

Mikhail S. BLINNIKOV

2.1. INTRODUCTION

Development of industry and agriculture in the Northwestern Caucasus has considerably effected vulnerable mountain ecosystems during the last decades. Constantly increasing public demand for land is threatening yet untouched landscapes and unique wildlife. The necessity of wilderness protection in the Caucasus requires sufficient knowledge of the history of regional ecosystems. In the present paper the attempt has been made to investigate the history of alpine communities using the paleoecological method of phytolith analysis (PIPERNO 1988).

The method yielded interesting results in numerous research works on plant community history throughout the world (CARBONE 1977). Many papers regard the history of wetlands, prairies, boreal and tropical forests and other ecosystems from the viewpoint of the phytolith analysis (BAKER 1959, WITTY and KNOX 1964, WILDING and DREES 1971, PALMER 1976, KISELEVA 1982, ANDREJKO and COHEN 1984, PIPERNO 1991).

Still, the works in which this method is applied to the histories of alpine communities are very rare. In this context, the possibility of using phytolith analysis in the study of alpine ecosystem history is investigated in this paper.

As expressed by ROVNER (1971), phytoliths exhibit three important features, enabling their use in paleoecology: they withstand decomposition, exhibit considerable morphological diversity and occur in the soil in sufficient quantities to reflect the nature of the entire parent community. Phytoliths composed of silicon dioxide or silica are one of the most durable plant fossils (PIPERNO 1991). They are very diverse in size, shape and colour, and therefore can reflect the diversity of parent plant species (e.g. METCALFE 1960, TWISS et al. 1969, BROWN 1984).

PIPERNO (1988) reports important data on phytolith occurrence in different plant taxa, including many tropical families. Despite certain limitations,

restricting wide-spread application of this method, it was quite workable under very diverse conditions. The first limitation is that not all plants are significantly, if at all, represented by adequate amounts of recognizable phytoliths. In the temperate zone, most articles chiefly concern grasses, sedges, composites and a few other families as principal phytolith producers. In many papers grasses are considered the main source of silica phytoliths in temperate communities (SMITHSON 1958, BLACKMAN 1971, KISELEVA 1982, BROWN 1984, DINESMAN et al. 1989).

Second, a single species of some taxa, e.g. grasses, can produce over a dozen different forms, complicating analysis. Therefore, it is crucially important to conduct research on a site-to-site basis, carefully examining local peculiarities of silica bodies distribution in plants (PIPERNO 1988). Keeping in mind these restrictions, reliable data on plant community history can be expected.

An impressive body of results on historical changes in the mountain environment and distribution of vegetation in the Holocene has been collected in the Caucasus in many recent research projects (MAKHOVA and PATYK-KARA 1961, TUSHINSKY 1962, SEREBRANY et al. 1980, SOKOLOVA 1982, MARGALITADZE and KIMERIDZE 1985, SAVINETSKY 1992). Most works deal mainly with broad scale transitions in climate and general changes in distribution of major vegetation types. Only a few articles discussed local historical changes in composition of particular plant communities (KHAPAEV 1976, PAVLOVA and ONIPCHENKO 1992). Probably, this gap is because the most widely used paleoecological method of pollen analysis usually provides data on a more broad than local level. Transition of pollen and spores by wind and alien pollen input from neighbouring communities can significantly distort local pollen spectra.

If applied in the study of open mineral soils instead of buried soils, pollen analysis is also seriously effected by the intensive processes of zoogenic and cryogenic disturbances and the high rate of destruction by soil reducers. It seems that phytolith analysis, being very effective specifically on a local scale, could be successfully applied to the investigation of a particular community history. Alpine conditions of the Northwestern Caucasus are probably favourable for phytolith preservation in soils because of the cold humid climate, acidic soils with high humus content and moderately low microbiological activity (MAKAROV 1985).

In the present work the attempt is made to apply phytolith analysis in the study of the history of four types of alpine communities. The task was: first, to find out, if phytoliths occur in alpine soils in quantities sufficient for analysis, second, to explore their distribution in soil profiles under four types of

communities and to draw phytolith diagrams, third, to interpret Holocene dynamics of different alpine communities from the viewpoint of phytolith analysis and fourth, to compare these results with data obtained earlier in the same place by means of pollen analysis (PAVLOVA and ONIPCHENKO 1992). We also tried to attribute phytolith forms, found in soils, to specific taxa of alpine plants (BLINNIKOV 1992).

Acknowledgement

We express our sincere gratitude to all members of the Moscow State University expedition in Teberda State Reserve for their help in gathering field materials. The author especially thanks N. Kiseleva and all staff members of the Laboratory of Historical Ecology of the Institute of Evolutionary Morphology and Ecology of Animals for providing laboratory techniques and consultations. Thanks also are due to I. Hammamenyuk for provided laboratory materials and the faculty members of the Dept. of Soil Sci. of MSU N. Dronova, T. Ulyanova, V. Ivanov and A. Smagin for guidance in the use of laboratory equipment. In particular, we thank A. Bobrov for his valuable assistance in taking SEM photographs and A. Golyeva for the useful comments on our Diploma thesis. The work was carried out under the the supervision of V. Onipchenko, whose kind assistance was constant and encouraging.

2.2. METHODS

Samples of plants and soils were gathered in the study area of Moscow State University on Mt. Malaja Hatipara, described in detail in Chapter 1 of this volume, in the following communities:

1. Alpine lichen heaths (ALH)
2. *Festuca varia* dominated grasslands (FVG)
3. *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM)
4. Snow bed communities (SBC).

We analyzed soil samples, taken from four soil profiles under four sample areas, namely ALH(U), FVG(U), GHM(L) and SBC(L) (see Chapter 1.4). A sample of about 100 g was taken from each soil layer in the following way: one sample per each 2 cm of soil profile from 0-2 to 8-10 cm, and one sample per each 5 cm from 10-15 cm to the lower limit of horizon B (25-40 cm dependent on community type).

Soils were treated according to the slightly modified method suggested by PIPERNO (1988). Thirty grams of sample soil were stirred in 15 ml of 4% solution of sodium pyrophosphate to loosen phytoliths from soil aggregates. The obtained suspension was sieved through a 250 μ m sieve to remove coarse

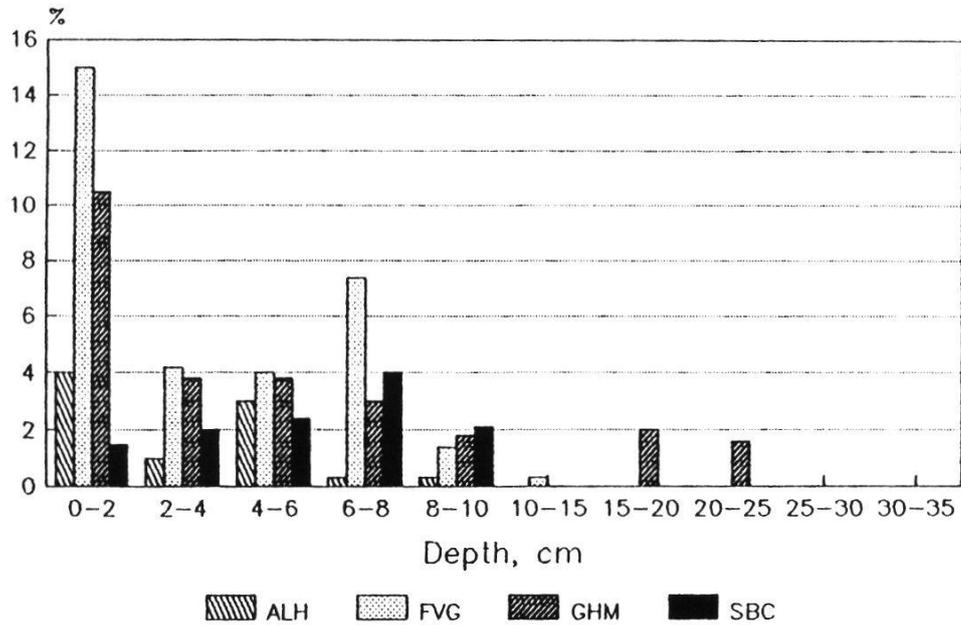


Fig. 2.1. Frequency of opal phytoliths in the silt fraction (10 -50 μm) of alpine soils in 4 communities (percentage of total number of grains in the fraction).

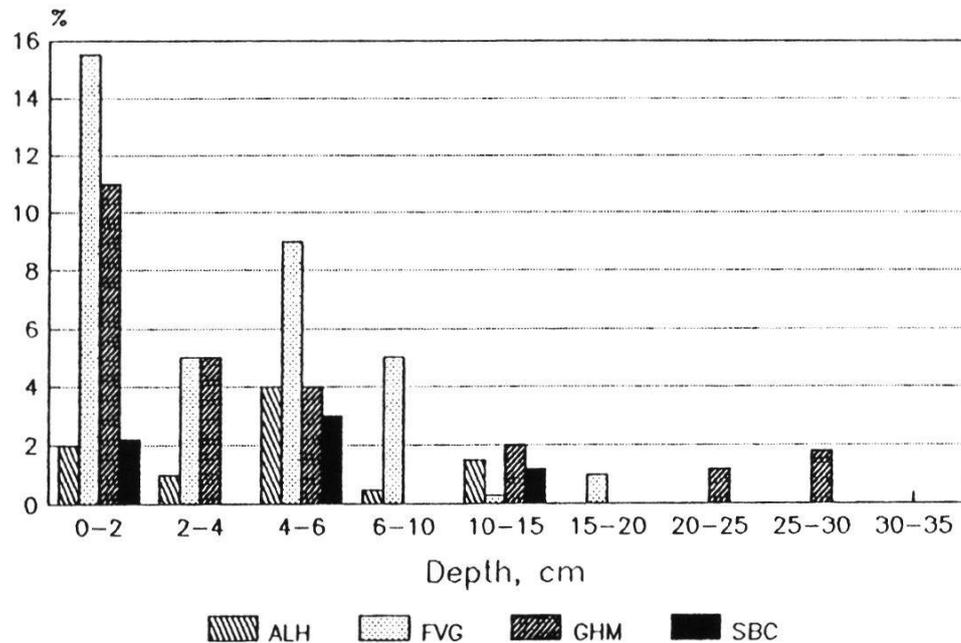


Fig. 2.2. Frequency of opal phytoliths in the fine sand fraction (50 -250 μm) of alpine soils in 4 communities (percentage of total number of grains in the fraction).

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Table 2.1. Percentage of major groups of phytoliths in alpine grasses, % of the total number of phytoliths in a species.

Species	hats	plates	wavy	long cells	hairs	bran. rods	scuti-form	sum of phytol.
<i>Agrostis vinealis</i>	12.5	9.5	21.0	32.0	6.5	-	-	266
<i>Alopecurus ponticus</i>	12.5	76.5	-	3.0	3.5	-	-	253
<i>Anthoxanthum odoratum</i>	2.5	60.0	15.5	7.0	15.0	-	-	74
<i>Briza marcowiczii</i>	5.0	5.0	81.0	5.0	-	-	-	238
<i>Bromopsis variegata</i>	<1.0	41.0	10.0	10.0	7.0	-	29.0	230
<i>Calamagrostis arundinacea</i>	-	32.0	23.5	35.5	7.0	-	-	127
<i>Catabrosella variegata</i>	59.0	36.0	-	4.0	-	-	-	122
<i>Deschampsia flexuosa</i>	65.0	22.0	-	3.0	2.5	-	-	145
<i>Festuca brunnescens</i>	90.5	6.0	-	2.0	-	-	-	162
<i>Festuca ovina</i>	80.0	15.0	-	3.0	<1.0	-	-	396
<i>Festuca varia</i>	88.0	1.0	-	9.5	<1.0	-	-	211
<i>Helictotrichon versicolor</i>	61.5	8.0	29.0	-	<1.0	-	-	231
<i>Nardus stricta</i>	89.5	1.0	-	6.0	-	3.0	-	412
<i>Phleum alpinum</i>	38.5	4.0	14.0	18.5	-	-	14.5	167
<i>Poa alpina</i>	53.0	44.0	7.0	13.0	9.0	-	-	161
<i>Trisetum flavescens</i>	18.0	56.0	3.5	16.5	<1.0	-	-	239

sand and plant tissues. Using the "dropper" method (VADYUNINA and KORCHAGINA 1986) and gravily sedimentation, clays were removed and fine sand (50-250 μm) and silt (10-50 μm) fractions were separated. The latter two fractions were washed with a 10% solution of hydrochloric acid to remove carbonates and other salts. Next samples were centrifuged at 2000 rpm for five minutes and washed then three times with distilled water. Organic matter was removed by adding concentrated nitric acid and potassium chlorate with subsequent boiling in sand a bath for one hour.

A heavy liquid solution of potassium and cadmium iodides, first used by CARBONE (1977), were used to extract phytolith from the samples. Specific gravity of the solution was about 2.1. Floating phytoliths were transferred to a polyethylene microfilter with pores of 1 μm diameter, then washed with distilled water and dried. Finally, phytoliths were examined in glycerine under petrographic and regular optical microscopes at 70 x to 600 x. In each sample, at least 200 phytoliths were counted, the amount considered sufficient by many authors (PIPERNO 1988). The percentage of phytoliths in the total number of soil grains in a sample (Fig. 2.1 and Fig. 2.2) and the percentage of different phytolith forms were determined (Fig. 2.3 and Table 2.2). The individual phytolith shapes were identified in reference to the table of phytolith content in different grasses of the alpine zone (Table 2.1), based on previous research (BLINNIKOV 1992).

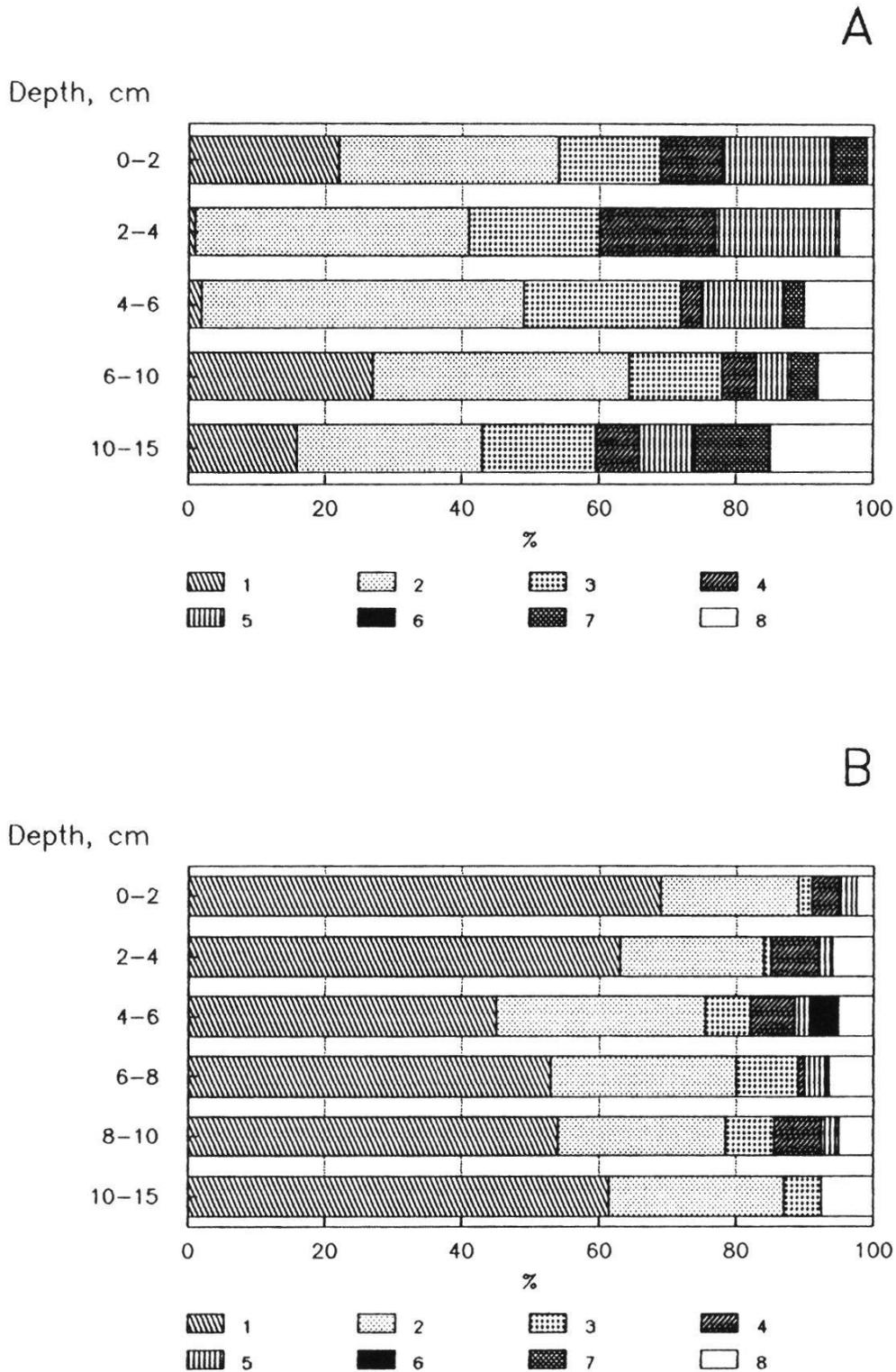
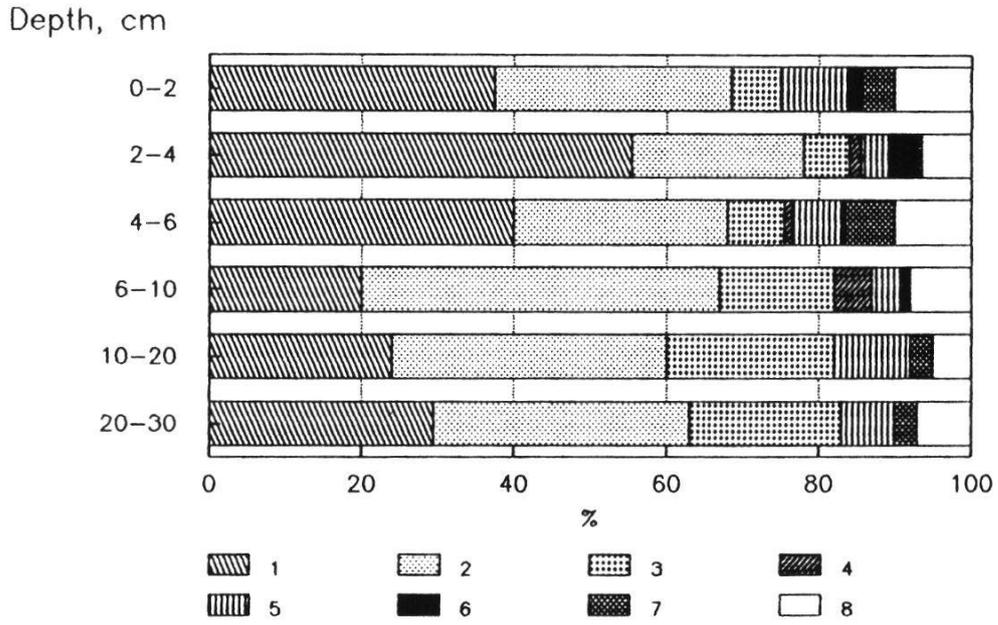


Fig. 2.3. Frequency of 8 major phytolith groups in alpine soil profiles under 4 communities: A = ALH, B = FVG, C = GHM, D = SBC; 1 = hats, 2 = straight-edge plates, 3 = wavy-edge plates, 4 = long cells, 5 = trichomes, 6 = branched rods, 7 = cone-shaped, 8 = other forms.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

C



D

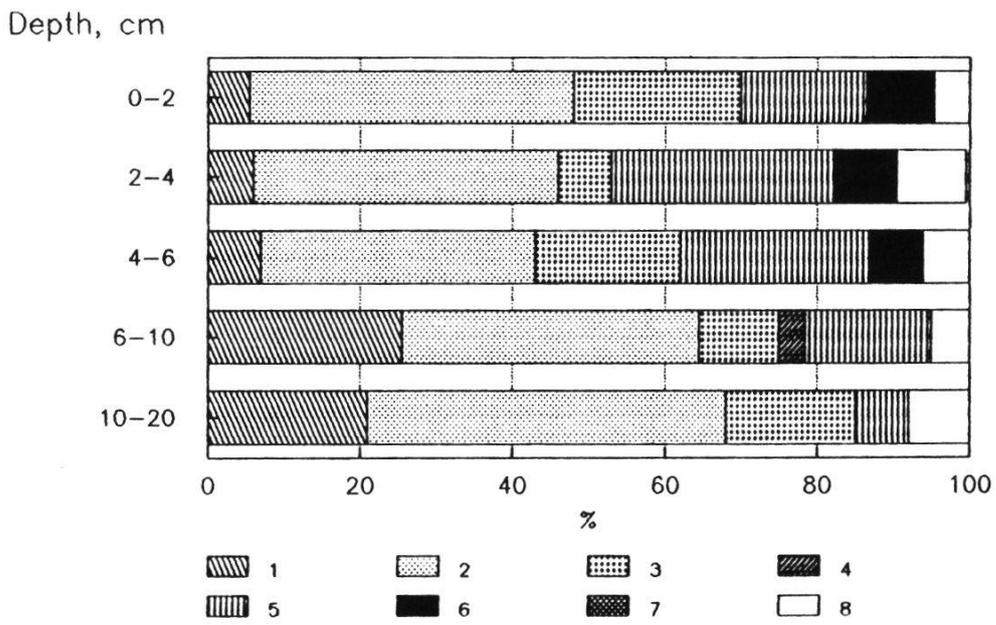


Fig. 2.3. (continued)

Table 2.2. Distribution of principal phytolith forms in 4 soil profiles under 4 types of alpine communities, % of total number of phytoliths in a horizon.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Phytolith principal forms (see fig. 2.5)	Profiles										
	ALH (Upper)					FVG (Upper)					
	0-2	2-4	4-6	6-10	10-15	0-2	2-4	4-6	6-8	8-10	10-15
1	19	1	2	10.0	8.0	67	59	41.5	46.5	40.0	60.5
2	3	-	-	17.0	8.0	<1	4.0	3.5	5.5	12.0	-
3	-	-	-	-	-	<1	-	-	1.0	-	-
4	-	-	-	-	-	<1	-	-	<1.0	2.0	1.0
5	12	31	29	21.0	11.5	8	4.0	13.0	17.0	14.0	15.5
6	3	-	1	2.0	-	4	2.0	8.0	2.0	<1.0	-
7	-	1	-	-	2.0	<1	1.5	-	-	2.5	-
8	3	-	-	2.0	<1.0	-	<1.0	2.0	-	-	1.0
9	11	5	15	8.5	13.5	-	3.0	-	-	-	-
10	-	3	-	-	-	-	-	-	-	<1.0	-
11	-	-	-	-	<1.0	1	1.5	-	<1.0	<1.0	1.0
12	3	-	2	4.0	<1.0	5	9.0	7.5	8.0	7.0	8.0
13	13	14	12	11.0	14.5	<1	-	3.0	5.0	-	5.5
14	2	-	-	-	-	1	<1.0	2.5	3.0	3.5	-
15	-	-	-	-	-	<1	<1.0	<1.0	<1.0	-	-
16	-	5	11	2.5	2.0	-	-	<1.0	<1.0	3.5	-
17	9	10	3	5.0	6.5	-	7.0	6.5	<1.0	4.5	-
18	-	7	-	-	-	4	-	-	<1.0	<1.0	-
19	-	-	-	-	-	-	-	4.0	<1.0	-	-
20	-	-	-	-	-	-	<1.0	<1.0	<1.0	-	-
21	4	-	-	3.5	-	2	1.0	1.5	-	-	-
22	10	7	7	1.5	5.5	<1	<1.0	-	2.0	<1.0	-
23	2	11	5	-	2.5	-	<1.0	1.0	1.0	2.0	-
24	-	-	-	<1.0	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-
26	-	-	3	-	-	-	-	-	-	-	-
27	5	-	3	4.0	11.0	-	-	-	-	-	-
28 others	1	5	7	8.0	14.0	3	5.0	5.0	4.5	5.0	-
Total number of phytoliths	103	100	100	117	111	355	310	310	271	114	102

Table 2.2. (continued)

Phytolith principal forms (see fig. 2.5)	Profiles						SBC (Lower)				
	GHM (Lower)						0-2	2-4	4-6	6-10	10-20
	0-2	2-4	4-6	6-10	10-20	20-30	0-2	2-4	4-6	6-10	10-20
1	2.0	5.5	3.5	2	-	7.0	-	-	-	8.5	-
2	35.0	49.5	36.5	17	24.0	21.5	5.5	3.5	7.0	17.0	19
3	-	-	-	-	-	1.0	-	2.5	-	-	1
4	<1.0	<1.0	-	1	-	-	-	-	-	-	1
5	7.5	8.5	15.0	23	11.5	20.5	25.5	23.0	20.0	20.5	21
6	1.5	1.5	-	1	11.5	-	10.0	8.0	10.0	7.0	4
7	4.0	1.0	-	1	1.5	1.0	-	4.5	1.0	1.0	8
8	1.5	<1.0	2.0	2	2.0	1.0	2.0	2.5	2.0	2.5	-
9	5.0	2.5	1.5	6	-	2.0	-	2.0	-	3.5	2
10	-	-	2.0	5	2.0	-	-	-	-	-	-
11	<1.0	-	-	1	-	2.0	-	-	-	3.5	9
12	6.0	7.5	6.0	6	4.0	5.0	5.0	-	1.0	-	-
13	4.5	2.0	5.5	4	7.5	8.0	<1.0	2.0	6.0	9.5	7
14	2.0	3.0	<1.0	10	6.5	5.0	21.5	4.5	8.0	-	6
15	-	-	<1.0	-	5.0	1.0	-	-	5.0	1.0	4
16	-	1.0	1.5	1	3.0	6.0	-	<1.0	-	-	-
17	<1.0	1.5	1.0	5	-	-	-	-	-	3.5	-
18	-	-	-	-	-	-	-	<1.0	-	-	-
19	1.5	3.5	<1.0	1	-	-	9.0	8.0	7.0	-	-
20	4.5	1.0	4.5	4	2.0	2.0	-	2.0	1.0	2.5	2
21	4.0	<1.0	5.5	2	5.0	5.0	4.5	6.0	3.5	3.5	2
22	2.0	2.0	1.0	<1	3.0	2.0	12.0	19.0	21.5	13.0	5
23	3.0	2.0	<1.0	2	2.0	-	-	4.5	-	-	-
24	-	-	-	-	-	-	-	-	-	-	-
25	-	-	1.0	-	-	-	-	-	-	-	-
26	-	-	<1.0	<1	-	-	-	-	-	-	-
27	4.5	<1.0	6.5	-	3.0	3.0	-	-	-	-	-
28 others	10.0	5.0	5.5	5	6.5	7.0	4.5	7.0	7.0	3.5	9
Total number of phytoliths	230	336	200	101	109	102	112	112	84	83	100

2.3. RESULTS

2.3.1. Principal phytolith forms found in alpine plants and soils

We found phytoliths in all 17 grasses and five sedges growing in the study area in the alpine zone (Table 2.1, also BLINNIKOV 1992). Besides that, a much fewer number of silica bodies was found in 15 out of 25 studied species of

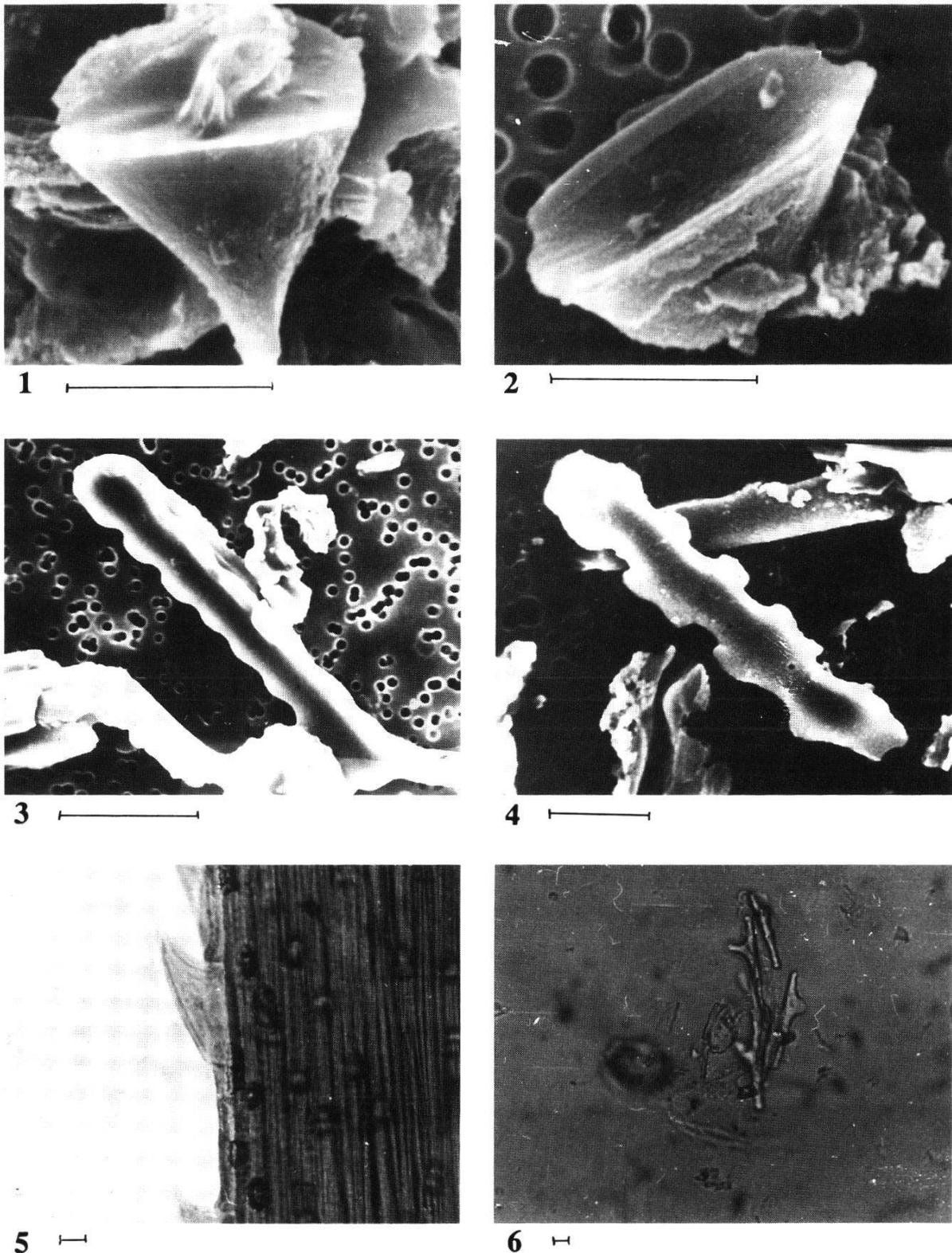


Fig. 2.4. Scanning electron microphotographs of phytoliths from alpine grasses. 1 = keel hat phytolith of *Festuca varia* (group of hats), 2 = simple hat phytolith of *Festuca ovina* (group of hats), 3 = wavy-edge phytolith of *Calamagrostis arundinacea* (group of wavy plates), 4 = lobed phytolith of *Calamagrostis arundinacea* (group of wavy plates), 5 = trichomes on the margin of the leaf of *Helictotrichon versicolor* (trichome group), 6 = branched rods of *Nardus stricta* (branched rod group). The scale is 10 μm .

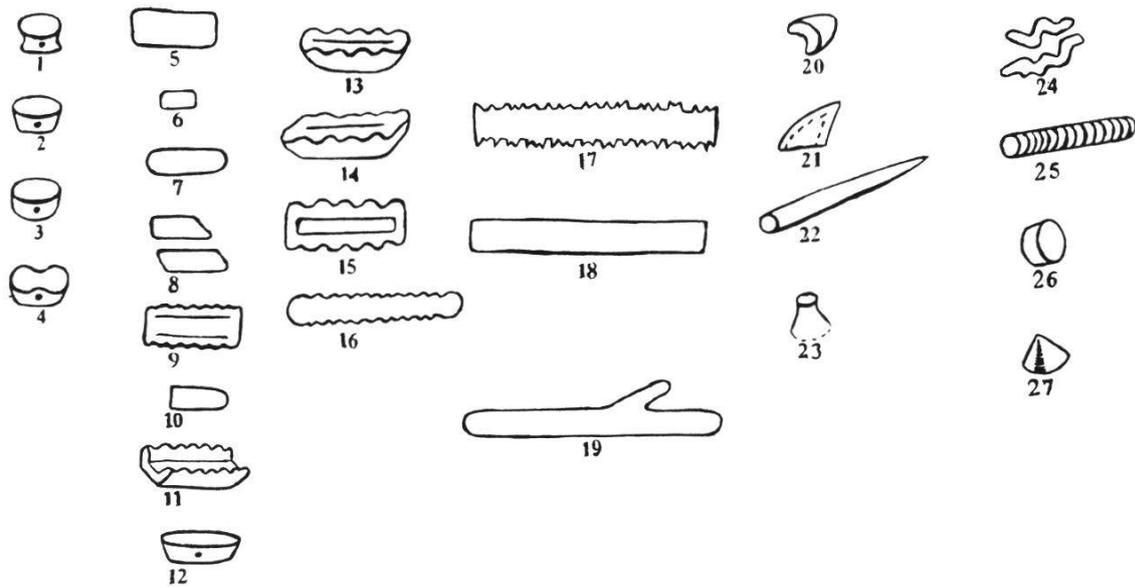


Fig. 2.5. Principal phytolith forms from alpine soils.

1-4 (group of hats): 1 = keel , 2 = simple, 3 = barrellike, 4 = pseudodumbbell; 5-12 (group of straight-edge plates): 5 = rectangular, 6 = small rectangular or round end, 7 = round end, 8 = slanting end, 9 = saw edge, 10 = one round end, 11 = trough, 12 = "boat" phytolith; 13-16 (group of wavy-edge plates): 13 = short with round ends, 14 = short with rectangular ends, 15 = lobed, 16 = long with round ends; 17-18 (long cell group): 17 = saw edge, 18 = straight edge, 19 = branched rods (*Nardus stricta*), 20 = spearheads; 21-23 (trichomes group): 21 = trichomes, 22 = hairs, 23 = hairbases, 24 = "hyphs", 25 = vessels, 26 = round plate, 27 = cone-shaped (*Carex* sp.).

other alpine vascular plants and in the two, most abundant lichens in the study area. Yet only grasses, sedges and, to a lesser extent, some haired dicotyledons, like composites, contributed noteworthy amounts of phytoliths into soil assemblages. In total, about 50 different forms were found in plant material.

However, several important dominants, like *Geranium gymnocaulon* and *Hedysarum caucasicum*, do not accumulate silica at all. Some other species bring certain phytoliths, but at a very insignificant level.

As already mentioned, phytoliths are very diverse in shape and form. Although several more or less fruitful attempts were undertaken (SMITHSON 1958, TWISS et al. 1969, BROWN 1984), there is no well-developed and widely adopted classification (either morphological or genetic) of grass phytoliths. The present work follows, in general, the morphological classification of KISELEVA (1992), which is close to the classification of BROWN (1984). About 30 different phytolith forms (Table 2.2) found in soils were combined into 8 distinct major groups (Fig. 2.4 and Fig. 2.5).

1. Hats (short trapezoids [BROWN 1984]). Phytoliths from short cells of grass epidermis, usually round if seen from above, but hat-like or triangular if

seen from the side (Fig. 2.4). The base of the hat is on the outer epidermal surface, and the apex is directed toward the inside of the leaf (BLACKMAN 1971).

2. Plates with straight edges (usually called rods by many authors [SMITHSON 1958, BLACKMAN 1971]). Forms usually appearing in the coastal regions of grass leaves. It seems feasible to distinguish this group from wavy and lobed plates (the following group).
3. Plates with wavy and lobed edges. Phytoliths called sinuous trapezoids by BROWN (1984). The latter two groups are very diverse, and there are phytoliths, with only slight "waves," which fall between.
4. Elongate phytoliths, usually having protrusions along their sides, from long cells of grasses (TWISS et al. 1969, BROWN 1984) and, possibly, from *Luzula* species.
5. Trichomes. In this group, both grass trichomes and hairs with hairs are combined and hair bases of dicotyledon species (chiefly *Compositae*, *Sibbaldia* and *Campanula*). This is to simplify the counting procedure, as it is sometimes difficult to distinguish the taxonomic origin of a hair found in soil. However, in Fig. 2.5 "trichomes" stands entirely for grass originated hairs, while "hairs," "hair bases" and some other forms represent phytoliths of uncertain origin.
6. Branched rods were first described by SMITHSON (1958) from British soils and found later by BAKER (1959) in Australia. They are clearly attributed to *Nardus stricta*, a species from the monotypic tribes *Nardeae*.
7. Conical phytoliths originating from sedges (MEHRA and SHARMA 1965, PIPERNO 1988).
8. Others. Mixed group of unrecognizable phytoliths.

2.3.2. Subrecent phytolith assemblages and present vegetation

Phytolith assemblages from the upper soil layer (0-2 cm) appeared to be quite different under all four community types. At the same time, phytolith frequencies in two fractions (fine sand and silt) were very similar (Fig. 2.1 and 2.2). ALH and SBC upper soil layer assemblages are poor in phytoliths (2-4% of the total number of grains in both fractions). GHM assemblage is richer (10-11 %), and that of FVG is the richest (15%).

It can be noted that these data closely resemble the distribution of above-ground phytomass of grasses and sedges in the four studied communities (ONIPCHENKO 1985, 1990). If all studied species produce phytoliths in direct

proportion to their aboveground phytomass, we can predict that, for example, under the community with the lowest grass and sedge phytomass (SBC 18 g/m²), the percentage of phytoliths must be the lowest among the four communities. ALH, therefore, must be about 2.7 times richer in phytoliths (81 g/m²), whereas GHM 4.5 times (132 g/m²) and FVG must be the richest community (13.6 times, or 245 g/m²). Results of direct counting of phytolith percentages in both studied soil fractions correspond well to the predicted ratio (Fig. 2.1 and Fig. 2.2).

Phytolith assemblage from the upper soil layer (0-2 cm) of the ALH(U) soil profile is characterized by almost equal content of hats, abundantly produced by *Festuca ovina*, and wavy rods, typical for *Helictotrichon versicolor* (Fig. 2.3a). The role of sedge phytoliths in this assemblage is less significant, but still about 5% of all phytoliths are conical sedge forms and 15% of the assemblage constitute trichomes (including also hairs, hair bases and prickles of various shapes). This points at the considerable number of haired species in the community (e.g. *Antennaria dioica*, *Campanula biebersteiniana*, *Erigeron uniflorus*).

The FVG(U) assemblage is especially rich in hats, for the most part having a distinctive keel (68% of all forms, Fig. 2.3b). Such phytoliths were found in abundance in the dominant species of this community (*Festuca varia*). The role of wavy phytoliths is negligible here (only 3%).

The GHM(L) profile in its upper layer (0-2 cm) also contains many hats, but for the most part lacking keels (35%). They originate from *Nardus stricta* or *Phleum alpinum* (Table 2.1), a species typical for this community type (see Chapter 1.4.3). Because it is so easy to confuse this form with keel hats, they were simply combined for the phytolith diagrams. Wavy forms and trichomes are also very common here. Their origin is probably *Agrostis vinealis* and *Phleum alpinum*.

The SBC(L) contribute lots of plates (42%) and wavy phytoliths (15%). Branched rods of *Nardus* (9%) were also found here. This plant is the most abundant grass species in this community (ONIPCHENKO 1990). A significant number of composites and other hairy species (*Gnaphalium supinum*, *Sibbaldia procumbens*) is stressed by the considerable amount of hairs and trichomes in the upper soil layer. In general, GHM recent assemblages are most diverse (seven major phytolith groups). FVG assemblage resembles the latter, but has only six groups with absolute prevalence of hats. ALH and SBC communities, being very different in their composition and habitat requirements (cf. Chapter 1.4), produce controversially similar assemblages with a

significant percent of trichomes, straight and wavy plates. Probably, certain difficulties will arise in distinguishing these two communities by phytolith analysis. Yet there is an important difference between them. ALH recent assemblage lacks branched rods, whereas that of SBC lacks conical phytoliths of sedges.

2.3.3. Phytolith frequencies in soil profiles under four alpine communities

Analysis of silica phytoliths has shown a considerable difference in their distribution in soil profiles under four communities. Diagrams were drawn based on analysis of the silt fraction, which contains most identifiable forms. However, distribution of phytolith frequencies is very similar in both studied fractions (fine sand, 50-250 μm , and silt, 10-50 μm). Ratio of phytoliths to the total number of grains in a fraction rapidly decreases with depth (Fig. 2.1 and 2.2). Phytoliths were found in countable numbers as deep as 15 cm under ALH, 20 cm under FVG and SBC and 30 cm under GHM. Below this level silica bodies become very infrequent and reliable data on the frequency of different groups becomes unattainable. Thus, phytoliths are common till the border between the A1 and B horizons or somewhat deeper.

These soil horizons were dated using the radiocarbon method (GRISHINA et al. 1987). The average estimated age was 2160 ± 80 years for ALH (10-25 cm), 3610 ± 80 for FVG (25-35 cm), 2950 ± 80 for GHM (19-30 cm) and 3630 ± 60 for SBC (16-25 cm). The real ages of the soils must be higher because of various exchange processes occurring in non-buried alpine soils (PAVLOVA and ONIPCHENKO 1992). The authors report that pollen and spores can be found in the same profiles even at 40 cm below the soil surface.

The deepest penetration of phytoliths under GHM can be at least partly explained as caused by the high rate of burrowing activity of voles and other digging animals, especially active in this community (Chapter 1). The number of damaged, broken or partially dissolved phytoliths increases with depth. While phytolith frequency under GHM decreases almost constantly with depth, ALH and FVG have a "peak" of phytolith content at 4-8 cm (Fig. 2.1). Phytolith frequency under the poorest phytolith producer, i.e. SBC community, shows a strong tendency to grow from 0-2 to 6-8 cm with subsequent decrease at 10-15 cm. The observed peaks correspond to those noted by PAVLOVA and ONIPCHENKO (1992) for grass pollen content in the same soil layers of the same profiles. Probably, at that time, the role of grasses in pre-SBC, FVG and ALH communities was higher than today.

2.3.4. Distribution of different forms of silica phytoliths in four soil profiles

Although alpine plants in the study area bring at least 50 different forms of phytoliths (BLINNIKOV 1992), we found only about 30 different forms of silica bodies in the soil (Table 2.2 and Fig. 2.5). This is possibly due to the instability of some phytoliths in the soil. In the lower soil layers (20 to 35 cm dependent on community type), no essentially new forms were found, compared to the upper layers. According to these investigations, the lower soil layers lacked forms originating from both deciduous trees and conifers (GEIS 1973, KLEIN and GEIS 1978). It confirms data obtained for the same territory with pollen analysis (PAVLOVA and ONIPCHENKO 1992), that herbaceous vegetation has existed in the study area for at least four thousand years.

In the profile under ALH(U) (Fig. 2.3), phytolith assemblage from the 0-2 cm (subrecent) layer greatly resembles that of 10-15 cm. The latter, radiocarbon dated as being 2160 ± 80 years old (CHERKINSKY unpubl. data), however, contains more conical phytoliths of sedges and fewer hats and trichomes. It can be assumed that this community has existed for at least two thousand years. At that time, it looked much like the present community. Nevertheless, in more recent times certain changes in its floristic composition have occurred. Hats are almost absent at 2-4 and 4-6 cm, while the percentage of trichomes remains constant, indicating perhaps, a colder and more humid climate (higher share of composites and lower of *F. ovina*), and can be set in to the XIII-XV centuries, i.e. the vernau glaciation stage (TUSHINSKY 1962). Wavy plates and trichomes are common through all profiles. This proves that *Helictotrichon versicolor*, which produces wavy forms, and haired species, like *Campanula biebersteiniana* and some composites, have played a significant role throughout the community history.

In the FVG(U) reliable data on phytolith relative frequencies below 15 cm could not be obtained, although the soil layer in this community is thicker than in the previous one. Obtained results (Fig. 2.3b) proved that the FVG had been existing for a long time (about 2000 years) with only slight changes in their composition. Keel hats of *Festuca varia* and other short phytoliths absolutely prevail in the upper layer. They become less frequent at 4-6 and 6-8 cm. At this depth, well recognizable branched rods of *Nardus stricta* were found along with a considerable quantity of wavy phytoliths, typical for many broad-leaf grasses (e.g. *Anthoxanthum odoratum*, *Calamagrostis arundinacea* and *Phleum alpinum*). The increasing role of mesophytic grasses can be

connected with a general increase in humidity in the Northwestern Caucasus 500 to 800 years ago in the vernau glaciation stage (TUSHINSKY 1962).

Therefore, the composition of pre-FVG communities was close to that of mesophytic alpine meadows like the present GHM (but possibly with dominants other than *Hedysarum* and *Geranium*): An increase of *Nardus stricta* must have been caused by intensive grazing, typical in the Northwestern Caucasus in that time (SAVINETSKY 1992). This species is usually avoided by sheep and serves as an indicator of grazing (SMITHSON 1958). Again, as in the previous case, the deepest assemblage (10-15 cm) is similar to the uppermost one. It seemingly represents vegetation of the so called "second xerothermic period" with dry conditions, occurred about 2000 years ago (TUSHINSKY 1962).

Thus, it is very probable that FVG developed through a herbaceo-grass stage, resembling the present *Geranium*-dominated meadows, although the role of *Festuca varia* always played a leading role, as there are more than 50% hat phytoliths in each horizon.

In the GHM(L) profile, assemblage (Fig. 2.3c) from the 2-4 cm layer falls somewhere between GHM and FVG recent assemblages. A few percent of the branched phytoliths of *Nardus stricta* indicate an important role played by this species in the nearest past of the community. Again it can be connected with severe grazing in the last two or three centuries (see above). Presence of more than 50% hats and lack of conical sedge phytoliths in this layer lead to the conclusion that very recently GHM were occupied by more xeric FVG-like communities. This corresponds to the data given in PAVLOVA and ONIPCHENKO (1992).

Deep layers are characterized by equal percentages of three major groups, namely hats, straight plates and wavy plates, with a smaller portion of sedge phytoliths and trichomes. Such assemblages lay between ALH and GHM. It is suggested that they represent hypothetical "parent" communities, having developed later into both GHM and ALH. Supposedly they included grasses, sedges and herbs, mixed in a certain proportion without strong dominants.

It is noted that GHM assemblages are least reliable among the four studied profiles as their composition has probably been seriously influenced by the burrowing activity of animals (see Chapter 1.4.3).

The 16-25 cm horizon of the SBC(L) profile, dated 3630 ± 60 (GRISHINA et al. 1987), significantly differs from the upper portion of the profile (Fig. 2.3d) in phytolith forms. The lower assemblage is dominated by plates (50%). Hats and wavy phytoliths are less abundant (20 and 17%, respectively), while

trichomes are rare. In general, this assemblage takes after assemblages from the lower part of the GHM profile, attributed to a hypothetical "parent" community (see above). Such a community could have occupied the territory of the present SBC in the dry period of the second xerothermic stage (TUSHINSKY 1962) two or two and a half millennia ago.

The assemblages at 2-4 and 4-6 cm possess a great deal of trichomes, which suggests the presence of some composites and other haired species in the vernau glaciation stage. Branched rods of *Nardus* are absent in the deep layers and emerge for the first time at 4-6 cm. This also indicates intensive grazing during the last few centuries. SAVINETSKY (1992) provides data that nomadic tribes had occupied the Northwestern Caucasus about 2000 years ago, resulting in a sharp increase in sheep grazing on mountain grasslands and meadows. No *Nardus* phytoliths were observed in the deep layers dated at more than 3000 years.

Thus, on the basis of these results, the following scheme of historical changes in the four alpine communities are suggested:

ALH: ALH → more humid ALH → ALH

FVG: FVG → mesophytic meadows with *Nardus stricta* → FVG

GHM: "parent" herbaceo-grassland → xeric meadows, close to present FVG → GHM

SBC: "parent" herbaceo-grassland communities → SBC

In general, the results of the phytolith analysis confirm and add to the independent results of the pollen analysis (PAVLOVA and ONIPCHENKO 1992). Phytoliths may provide interesting paleoecological data on the local history of the alpine ecosystems.

SUMMARY

The history of four types of alpine communities in the Northwestern Caucasus was studied, using the method of phytolith analysis. All 4 communities produce silica phytoliths, chiefly of grass and sedge origin, in quantities sufficient for the analysis. The phytolith content in the subrecent assemblages (0-2 cm) can range from 1.8% of the total number of grains in silt and fine sand fractions under snow-bed communities to 15.5% under grasslands. The data obtained on phytolith frequencies in the subrecent assemblages closely correspond to the above-ground phytomass distribution of grasses and sedges among four communities.

Subrecent phytolith assemblages of four communities significantly differ. The alpine lichen heath (ALH) assemblage has approximately equal percentages of *Festuca ovina* hats and straight and wavy plates of *Helictotrichon versicolor*. There is also a significant percentage of trichomes, ostensibly produced by *Antennaria dioica*, *Campanula biebersteiniana* and other dicotyledon species. The grassland (FVG) assemblage is characterized by the overwhelming prevalence of keel hats of *Festuca varia* (68%). The shares of

trichomes and wavy plates are negligible. The alpine meadow (GHM) assemblage is the most diverse. It contains approximately equal percentages of hats and plates (about 35% each) as well as a considerable percentage of wavy plates, conical forms and trichomes. There is also a low percentage of branched rod phytoliths of *Nardus*. The assemblage of the snow bed communities (SBC) contains few hats and many wavy and straight edge plates, in addition to a lot of trichomes (of *Sibbaldia* for the most part). There are 10% branched rods in the assemblage, because *Nardus* is the most widespread grass in the SBC.

Phytoliths are not equally distributed in soils. In general their frequency decreases with depth. At a certain point their quantity becomes insufficient for reliable analysis, yet we can trace the history of the alpine communities for at least the last three thousand years. The composition of the lower assemblages differs from subrecent ones. However, no new forms were found, essentially dissimilar with those found in the subrecent assemblages. No traces of any arboreal phytoliths were detected. Apparently, the study area has not been occupied by forest vegetation during the last half of the Holocene and the alpine communities have been quite stable. A scheme of historical changes in the four studied communities is presented.

Under FVG, GHM and SBC *Nardus stricta* phytoliths were found in large quantities, indicating a severe grazing period in the recent history of the communities (several hundred years ago).

3. Experimental research of alpine communities with use of reciprocal transplantations

Andrej V. SENNOV and Vladimir G. ONIPCHENKO

3.1. INTRODUCTION

The main question of plant ecology can be stated as "What prevents certain species of plants from living in certain places?" In the broadest sense this question could be answered in two ways. First, some species cannot occupy a place merely due to historical reasons. Second, the species' survival in the community can be opposed by present ecological factors, both biotic and abiotic.

The transplantation method has been used for plant community investigation for a long time. At first, it was applied for separate plant individuals and in this form was rather widespread. Transplanted plants were often used as phytometers. Research carried out by BONNIER (see CLEMENTS 1905) was probably among the earliest, to use the phytometer technique. In the early twentieth century, CLEMENTS (1905) expounded general directions for experimental investigations of plant communities. Among those techniques the method of introduction of new species into an alien community occupied a prominent place. Later, CLEMENTS and HALL (1918) described this method as useful in the research of competitive relationships between plant species. Development of the turf cut transplantation method instead of transplantations of plant phytometers was started in 1910 by CLEMENTS. The basis of this method was documented by the year 1924 (CLEMENTS and WEAVER 1924).

To define whether conditions of growth and the natural habitat of a species are optimal, it is necessary to consider a rate of its competition with other species (ELLENBERG 1953, 1954). SHENNIKOV (1942) used pieces of cut turf, transplanted from one plant community to another to estimate the influence of interspecific competition on the viability of plant a species, i.e. narrowing its of potential ecological niche. As a result of this investigation, SHENNIKOV concluded that it is possible to distinguish two kinds of natural areals and eco-

logical optima (which are usually comparable); with interspecific competition and without. The former was called "ecological," and the latter "phytocoenotic" optimum. SHENNIKOV (1942) proved that there was a significant divergence between "ecological" and "phytocoenotic" areal for some species. Later ELLENBERG (1953, 1954) used the terms "physiological" and "ecological" areal to describe the range of ecological conditions in which species can grow without and with interspecific competition, resp. To avoid confusion between SHENNIKOV and ELLENBERG's terms, RABOTNOV (1983) suggested "auto-" and "synecological" areal and optimum for the same phenomena. Independently, in the field of general ecology, the same things have been called "fundamental" and "realized" ecological niches resp. (HUTCHINSON 1958).

It seems that the field transplantation technique is one of the best methods suited for the research of species coexistence mechanisms and behaviour of plant species under different ecological conditions. Unfortunately, only a few publications describing the usage of this method are known to the authors (GIGON 1971, KLÖTZLI 1980; MAY et al. 1982, DEL MORAL 1983, PARTRIDGE and WILSON 1988). It seems strange that this method, although very simple, available and important, has not found widespread application (PIGOTT 1982, RABOTNOV 1987b). Probably, this can be connected with the fact, that this method is very time consuming, since it is necessary to observe the transplanted pieces of cut turf for at least several years in order to obtain reliable results. During the first years of the experiments only transient dynamics of a community can be observed (TILMAN 1988). A new ecological equilibrium can be established after several generations of main dominants (LIKENS 1987).

A main purpose of this investigation was to find out how much recent environmental conditions are favourable for both existing and brought in plant species, or in other words, to determine the role of biotic and abiotic factors in maintaining the structure of some alpine communities. Elucidation of this problem also may be reached by investigating of reactions of different species to the changes in their environment caused by their introduction into other types of communities, which differ in their ecological parameters.

Acknowledgements

We wish to thank I. Malyshev for the field assistance.

3.2. METHODS

The experiments included reciprocal transplantation of turf cuts between four investigated communities:

- a) alpine lichen heaths (ALH)
- b) *Festuca varia* dominated grasslands (FVG)
- c) *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM)
- d) snow bed communities (SBC).

These communities are described in chapter 1 of this volume.

Within each community a rectangular experimental area of 8x13 m was selected, with its shorter side parallel to the base of the mountain. Areas with homogeneous vegetation were selected.

Within each area, rows of squares, 50x50 cm with 1 m spacing between them, were chosen in such way that the squares included most characteristic species of the community. The chosen squares formed eight rows with five squares in each (Fig. 3.1). Sample plots of 25x25 cm were marked within each square by means of aluminium tent-pegs and fishing line for shoot number counting.

The 160 squares (40 squares per community) obtained in this manner were distributed in the following way: Ten squares in each community were used as a control and the other 30 were transplanted by tens into three other communities in a random manner.

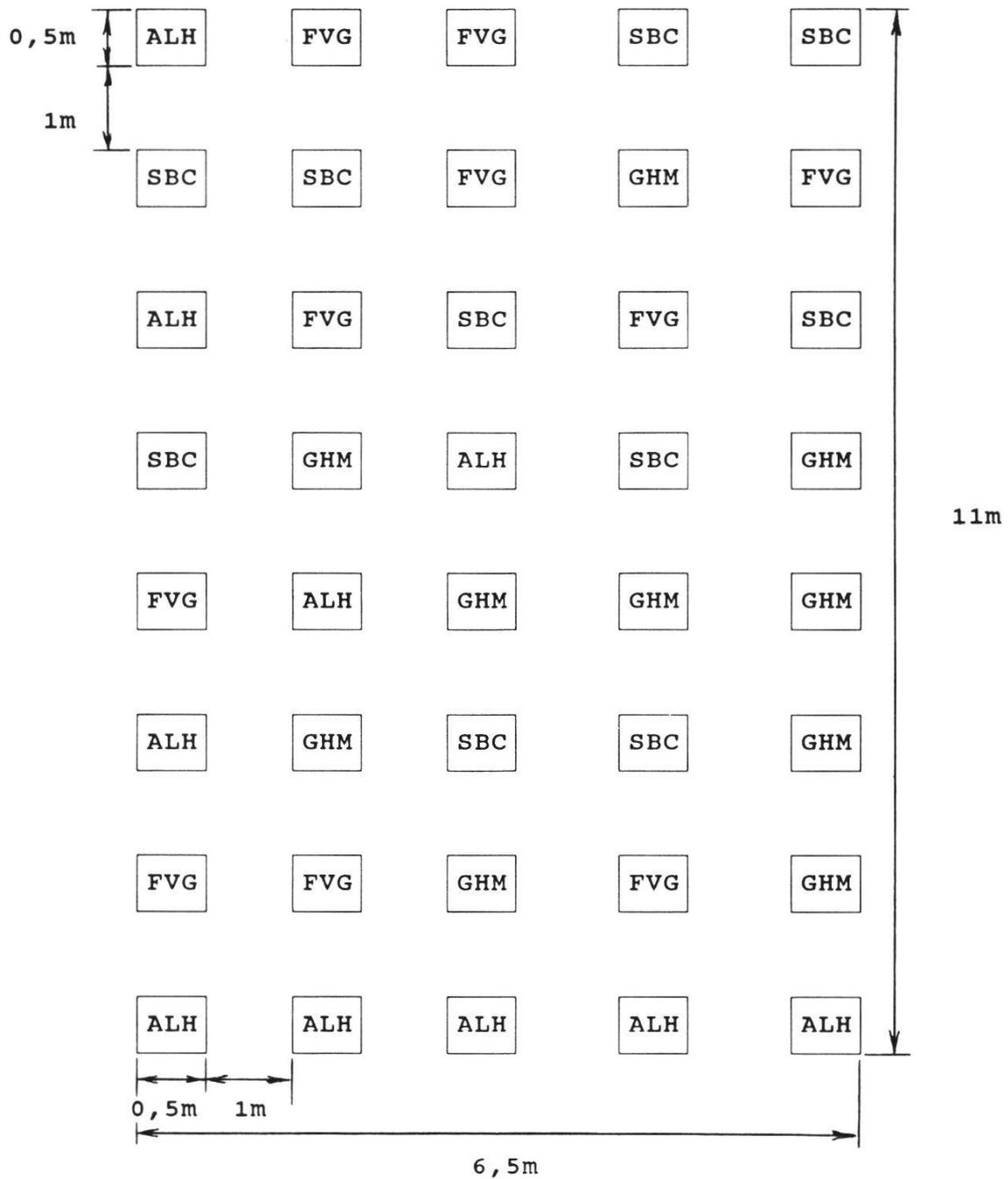
The translocations were carried out as follows: each transplanted sod was dug out as deep as the humus layer (approximately 15-25 cm). Then the turf cut was exchanged with a cut from another community.

The periphery surface of the turf cuts were wrapped with polyethylene stripes to prevent lateral penetration from roots of the surrounding plants, avoiding the additional influence of root competition.

The control squares were also dug out, wrapped around the edges in the same way, and turned around 180 degrees, and put back into the previous place.

The translocations were conducted during two weeks in the summer of 1989. Counting of plant shoots was started in 1988 and continued each subsequent year until July and August of 1992. The vegetative and generative shoots of each species were counted as well as juvenile individuals. Plants with small leaves and which were supposedly in the early stages of development or had low vitality were considered as juvenile individuals.

Fig. 3.1. Scheme of the experimental area in alpine lichen heaths (ALH).



The data resulting from 5 years of counting were evaluated in the following manner. For each type of translocation and control experiment the total amount of individuals of each plant species for each year was calculated. For species with unidirectional changes within four years (either increasing or decreasing amounts) a ratio between the total plant shoots during the last year of observations (1992) and the total during the year of transplantation (1989) for each square was calculated for each square:

$$R = \frac{\text{Sum in 1992}}{\text{Sum in 1989}}$$

average value of this ratio for each species and standard error of the average value.

The calculated data made it possible to detach random oscillations of quantity from naturally determined data using the t-test (a comparison with the initial condition).

A relative coefficient (K) was used to compare plant response to translocations with a control:

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

N_{t1} is the shoot density on experimental plots at the beginning of the experiment (1989), N_{t2} -shoot density on the experimental plots after some years (e.g. 1992), C_{t1} -shoot density on the control plots at the beginning of the experiment, C_{t2} - the same as in the $t2$ period. The coefficient, discussed in chapter 7, was counted only when all density parameters exceeded 10.

Morphological changes of one species were studied from each community: *Helictotrichon versicolor* from ALH, *Festuca varia* from FVG, *Geranium gymnocaulon* from GHM and *Taraxacum stevenii* from SBC. The length of the longest leaf in several *Helictotrichon versicolor* and *Taraxacum stevenii* plants and the height of generative shoots of *Geranium gymnocaulon* and *Festuca varia* were measured. Both control and transferred experimental plots were studied and a total of at least 30 measurements was carried out in each community. Based on these data, average values and standard error were calculated. To detach the reliable values from the insignificant, the t-test was used.

3.3. RESULTS AND DISCUSSION

3.3.1. Transplantations of alpine lichen heaths (ALH)

There were slight changes in the floristic composition of experimental and control plots after transplantations of ALH sod (Table 3.1 and 3.2). Only a few rare species (*Anthyllis vulneraria* on control, *Alchemilla caucasica* and *Gentiana biebersteinii* after transplantation to GHM) were no longer found

Table 3.1. Dynamics of shoots in the ALH, in the control and transplanted to SBC variants for four experimental years.

Used abbreviations: v = vegetative shoots, g = generative shoots, j = juvenile plants. Probability of distinction between the initial (1989) and 1992 years (t-test): * p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, SBC = snow bed communities.

Year	ALH-Control				ALH→SBC				
	89	90	91	92 t	89	90	91	92 t	
<i>Anemone speciosa</i>	v	26	19	20	16 *	19	22	26	25
<i>Arenaria lichnidea</i>	v	81	65	70	58	117	115	139	139
<i>Campanula</i>	v	44	39	45	56	39	41	34	56
<i>biebersteiniana</i>	j	39	42	36	43	44	39	41	41
<i>Campanula collina</i>	v	28	76	62	66 *	22	31	28	32
<i>Carex umbrosa</i>									
+ <i>C. sempervirens</i>	v	138	151	175	184 **	174	182	229	339 **
<i>Carum caucasicum</i>	g	10	7	8	9 *	9	7	6	10
	j	24	33	31	35	36	27	61	49
<i>Eritrichium</i>	v	21	41	40	15	14	10	8	5 ***
<i>caucasicum</i>	j	30	26	34	48	8	12	13	8 ***
<i>Euphrasia ossica</i>	g	102	84	26	47 *	106	13	46	4 ***
<i>Festuca ovina</i> (x10)	v	67	69	90	111 ***	55	57	69	128 ***
	g	11	8	53	42	10	0	6	63
<i>Gentiana djimilensis</i>	v	86	89	91	79	45	42	82	95
<i>Helictotrichon</i>									
<i>versicolor</i>	v	54	51	46	71	48	45	33	62
<i>Minuartia circassica</i>	v	34	26	24	2	97	103	72	112 ***
	g	3	1	3	21	9	0	3	2 ***
<i>Plantago saxatilis</i>	v	16	4	7	5 ***	6	1	2	4
<i>Ranunculus oreophilus</i>	v	15	19	21	21	6	7	18	10
	g	3	6	5	8	20	15	10	14
<i>Trifolium polyphyllum</i>	v	92	82	86	95	13	26	51	62
<i>Vaccinium vitis-idaea</i>	v	478	373	393	470	554	176	82	76 ***
Sum of shoots (x10)		231	228	253	282	227	179	199	281
Number of species:									
general		25	27	28	28	29	32	33	35
appearing		-	4	2	1	-	4	2	3
disappearing		-	2	1	1	-	1	1	1

2-3 years after the beginning of the experiment.

The ALH species fall into three groups according to their response to transplantations (Tab. 3.9).

- 1) Shoot density of the main dominants (*Festuca ovina*, *Carex umbrosa* and *C. tristis*, *Antennaria dioica*, *Trifolium polyphyllum*) and variegated oat (*Helictotrichon versicolor*) increased considerably when transplanted into

Table 3.2. Dynamics of shoots in the ALH transplanted to GHM and FVG variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

Year	ALH→GHM					ALH→FVG				
		89	90	91	92 t	89	90	91	92 t	
<i>Anemone speciosa</i>	v	20	14	17	14 *	22	20	22	20	
	g	11	8	10	10	7	13	3	6	
	j	7	15	10	8	7	14	14	4 **	
<i>Antennaria dioica</i>	v	126	139	107	151	86	93	113	135 *	
<i>Campanula biebersteiniana</i>	v	53	45	60	70	34	39	113	49	
	g	16	11	10	16	7	5	1	8 *	
	j	4	27	18	14	50	27	31	24	
<i>Campanula collina</i>	v	52	94	80	84 **	32	48	49	57 ***	
<i>Carex umbrosa</i> + <i>C. sempervirens</i>	v	122	165	213	381 ***	184	225	239	367 ***	
<i>Carum caucasicum</i>	v	18	10	8	5 **	6	4	7	6	
	j	22	75	29	38	26	63	38	14	
<i>Eritrichium caucasic.</i>	v	23	16	3	2 ***	28	21	15	15	
<i>Euphrasia ossica</i>	g	137	50	15	23 ***	94	40	4	4 ***	
<i>Festuca ovina</i> (x10)	v	51	74	102	144 ***	69	76	110	221 ***	
	g	28	4	70	78	30	9	116	95	
<i>Gentiana djimilensis</i>	v	100	55	35	59	133	89	75	64 *	
<i>Helictotrichon versicolor</i>	v	65	75	93	167 ***	62	61	85	112	
<i>Luzula spicata</i>	v	15	18	27	43 *	10	11	22	21	
<i>Pedicularis chroor.</i>	v	7	1	1	1 ***	1	3	0	1	
<i>Ranunculus oreophilus</i>	v	16	18	15	15	15	13	10	27	
	j	14	25	27	28	23	29	19	10 *	
<i>Trifolium polyphyllum</i>	v	40	43	32	32	56	88	81	81	
<i>Vaccinium vitis-idaea</i>	v	434	356	104	84 ***	544	492	174	105 ***	
Sum of shoots (x10)		199	220	219	300	232	238	249	359	
Number of species:										
general		28	31	33	33	28	31	32	32	
appearing		-	5	3	1	-	4	3	3	
disappearing		-	2	1	1	-	1	2	3	

the more productive FVG and GHM (Table 3.9). Apparently, these species have different syn- and autoecological optima and can grow successfully under the more favourable conditions of alpine grasslands and meadows without the competition of more vigorous plants (*Festuca varia*, *Nardus stricta* et al.).

2) Long living semirosette plants (*Anemone speciosa* and *Campanula bie-*

Table 3.3. Dynamics of shoots in the FVG, in the control and transplanted to SBC variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. FVG = *Festuca varia* dominated grasslands, SBC = snow bed communities.

Year	FVG-Control				FVG→SBC				
	89	90	91	92 t	89	90	91	92 t	
<i>Anthemis iberica</i>	v	1	2	3	1	20	13	23	43
<i>Antennaria dioica</i>	v	9	18	26	26	14	11	10	16
<i>Anthoxanthum odoratum</i>	v	35	37	67	96 *	28	20	58	119 *
<i>Campanula collina</i>	v	4	6	5	7	17	25	26	23
<i>Carex atrata</i>	v	9	5	8	18	2	5	6	0
<i>Festuca brunnescens</i>	v	47	59	53	54	29	22	71	47 *
<i>Festuca ovina</i>	v	148	214	377	297	234	168	115	140
	g	6	2	31	5	17	1	2	1 *
<i>Festuca varia</i> (x10)	v	154	175	256	315 ***	218	173	169	250
	g	126	14	69	21 ***	95	13	13	53
<i>Gentiana djimilensis</i>	v	13	11	12	14	34	14	25	34
	g	0	8	3	7	2	13	1	2
<i>Deschampsia flexuosa</i>	v	102	83	87	57	221	194	122	239
<i>Minuartia aizoides</i>	v	141	237	213	220	63	43	88	144 **
	g	10	8	8	0	0	1	2	3
<i>Nardus stricta</i> (x10)	v	108	141	165	217 *	115	86	72	96
	g	65	46	42	54	9	5	10	12
<i>Scorzonera cana</i>	v	13	15	9	8	19	21	16	25
	g	0	1	3	0	10	4	7	5
	j	0	2	4	3	4	10	9	6
<i>Viola oreades</i>	v	18	10	1	2 ***	31	21	3	6 ***
Sum of shoots (x10)		340	398	530	626	430	330	314	451
Number of species:									
general		21	23	22	21	23	27	28	25
appearing		-	4	1	1	-	6	3	2
disappearing		-	2	2	2	-	2	2	5

bersteiniana) demonstrated a significant tolerance to different ecological conditions. Their shoot density did not noticeably change, but the number of plants with generative shoots decreased and one without generative shoots increased in most experimental variants. It is believed that the ecological conditions of ALHs are more favourable for these species than the conditions of other communities. A longer observation period is necessary to prove this suggestion.

- 3) A few typical but minor components of the ALH (*Vaccinium vitis-idaea*, *Eritrichium caucasicum*, *Euphrasia ossica*) demonstrated negative

Table 3.4. Dynamics of shoots in the FVG transplanted to GHM and ALH variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

Year	FVG→GHM				FVG→ALH			
	89	90	91	92 t	89	90	91	92 t
<i>Anthoxanthum odoratum</i>	v 47	67	96	134 *	44	46	54	61
	g 3	7	9	4 *	4	7	13	5
<i>Campanula biebersteiniana</i>	v 6	15	13	15	0	0	4	1
<i>Campanula collina</i>	v 7	10	7	9	6	13	14	16
<i>Carex umbrosa</i>	v 0	0	7	13	13	1	13	15
<i>Euphrasia ossica</i>	g 0	1	0	1	0	3	2	8
<i>Festuca brunnescens</i>	v 99	104	216	200	58	58	60	87 ***
	g 25	5	40	4 ***	3	4	15	6
<i>Festuca ovina</i>	v 78	93	80	78	47	48	127	103
<i>Festuca varia</i> (x10)	v 135	163	226	349 ***	179	200	169	171
	g 103	14	107	106	85	47	216	24 ***
<i>Gentiana djimilensis</i>	v 0	14	14	8	48	40	59	63 **
<i>Leontodon hispidus</i>	v 10	18	8	7	14	16	9	2 ***
<i>Deschampsia flexuosa</i>	v 202	426	722	772 **	180	259	243	287 *
	g 20	0	11	15	3	5	22	2
<i>Minuartia aizoides</i>	v 42	76	58	42	210	125	133	159
<i>Nardus stricta</i> (x10)	v 57	114	106	110	86	122	98	81
<i>Ranunculus oreophilus</i>	v 4	7	3	0	2	8	5	4
	j 0	1	14	16	12	7	11	10
<i>Scorzonera cana</i>	v 29	37	19	17 *	21	38	21	15
	j 0	1	7	7	9	1	30	11
<i>Viola oreades</i>	v 71	0	2	0	37	7	16	26
Sum of shoots (x10)	274	375	485	614	350	398	379	349
Number of species:								
general	23	25	25	23	21	22	23	23
appearing	-	6	2	2	-	2	2	1
disappearing	-	4	2	4	-	1	1	1

responses to transplantation to all other communities. There is a good correlation between their experimental behaviour and natural distribution among the communities (Tab. 3.9).

There seems to be two main causes for the relative decrease of species performance in the experimental plots. First, the new microclimate (for example, the length of vegetative season, temperature regime etc.) can be less favourable than the original. Second, some ALH plants can increase their competition ability and suppress other components of the ALH more seriously. The

reason for this could not be distinguished within these experiments.

Apparently, the first cause is more important for the first years of the experiment because the process of transplantation is accompanied by disturbances. The reaction of most species is somewhat slow in the alpine zone, so competition relationships can be weakened for several years. The attempt was made to minimize the influence of the surrounding vegetation by means of root isolation and wide borders between the investigated plots and the original community. In spite of this, some aboriginal species did infiltrate the experimental plots of ALH, e.g., *Agrostis vinealis*, *Carum alpinum*, *Catabrosella variegata*, *Sibbaldia procumbens* in SBC; *Geranium gymnocaulon*, *Hedysarum caucasicum* and *Matricaria caucasica* in GHM; *Agrostis vinealis*, *Carum alpinum*, *Geranium gymnocaulon*, *Viola oreades* in FVG. They infiltrated the plots mainly by seeds and some of them by rhizome. The total floristic diversity of the plots increased slightly (Tab. 3.1 and 3.2). These observations support the suggestion that competition is not very strong during the first years after transplantation and some species can show their potential responses to the ecological conditions.

The same reasoning can be applied to the species which increase their performance on the experimental plots. In all cases, the behaviour of species under conditions of "depleted" competition can be estimated.

Of course, there can be other reasons for changes in species composition on transplanted plots such as the influence of consumers, apparent competition (CONNEL 1990) and others. More detailed experiments should be carried out to study these processes.

3.3.2. Transplantations of *Festuca varia* dominated grasslands (FVG)

Festuca varia and *Nardus stricta* are the main dominants of FVG. These species display very similar behaviour on experimental plots (Table 3.3, 3.4, 3.9). Shoot density of the species did not change significantly according to control when transplanted to GHM, but it decreased approximately twice when transplanted to a more severe environment like ALH or SBC. So it can be suggested that the auto- and synecological optima of the species are similar.

The behaviour of other FVG-species varies. *Deschampsia flexuosa* and *Festuca brunnescens* displayed positive reactions when transplanted to other communities. It is interesting that the species are very rare or absent in ALH, but their shoot density increases in this community. Apparently, severe

ecological conditions are less important for the species than the influence of main dominants (*Festuca varia* and *Nardus stricta*).

Anthoxanthum odoratum responded the same to transplantation to GHM as to control treatment. The shoot number decreased when transplanted to ALH, but slightly increased in SBC. *Minuartia aizoides* reacted positively to transplantation to SBC, where it is one of the most abundant species.

Floristic diversity of the experimental plots remained almost constant during the period of observation. A few rare species disappeared from the plots, for example: *Anthyllis vulneraria*, *Carex atrata*, *Matricaria caucasica* in SBC; *Anthyllis vulneraria* and *Viola oreades* in GHM. And a few new species appeared, for example: *Carum caucasicum*, *Sibbaldia procumbens*, *Taraxacum stevenii* in SBC; *Campanula biebersteiniana*, *Carum caucasicum*, *Euphrasia ossica*, *Pedicularis chroorrhyncha* in ALH. In the first year after transplantation, juvenile individuals of *Geranium gymnocaulon* and *Hedysarum caucasicum* had infiltrated from the surrounding GHM, but they died in the following year. So the structure and composition of FVG stayed very conservative under similar ecological conditions of GHM. It seems that *Festuca varia* has the similar competitive ability under GHM conditions as in its original community.

3.3.3. Transplantations of *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM)

This community type has properties similar to FVGs. Many species can grow in both GHMs and FVGs, but with differing frequency (Table 3.9). Still, the reaction of the GHM species to the transplantation differed from that of the FVG. The shoot density of most GHM species did not considerably change or even slightly increased when transplanted to similar communities (FVG and SBC, but decreased seriously when transplanted to more severe conditions of ALH, Tables 3.5, 3.6, 3.9). Such behaviour is typical for *Hedysarum caucasicum*, *Anthoxanthum odoratum*, *Minuartia aizoides*, *Veronica gentianoides*, *Scorzonera cana*, *Carum meifolium*. The ecological conditions of GHMs are almost favourable for these species, but they can be slightly suppressed by the main dominant *Geranium gymnocaulon*.

Geranium gymnocaulon displayed a significant tolerance to the wide spectrum of ecological conditions. The shoot density of this species did not change greatly in any variants (Table 3.9). By means of several morphological features of *Geranium gymnocaulon*, it was possible to ascertain that the

Table 3.3. Dynamics of shoots in the FVG, in the control and transplanted to SBC variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. FVG = *Festuca varia* dominated grasslands, SBC = snow bed communities.

Year	FVG-Control				FVG→SBC				
	89	90	91	92 t	89	90	91	92 t	
<i>Anthemis iberica</i>	v	1	2	3	1	20	13	23	43
<i>Antennaria dioica</i>	v	9	18	26	26	14	11	10	16
<i>Anthoxanthum odoratum</i>	v	35	37	67	96 *	28	20	58	119 *
<i>Campanula collina</i>	v	4	6	5	7	17	25	26	23
<i>Carex atrata</i>	v	9	5	8	18	2	5	6	0
<i>Festuca brunnescens</i>	v	47	59	53	54	29	22	71	47 *
<i>Festuca ovina</i>	v	148	214	377	297	234	168	115	140
	g	6	2	31	5	17	1	2	1 *
<i>Festuca varia</i> (x10)	v	154	175	256	315 ***	218	173	169	250
	g	126	14	69	21 ***	95	13	13	53
<i>Gentiana djimilensis</i>	v	13	11	12	14	34	14	25	34
	g	0	8	3	7	2	13	1	2
<i>Deschampsia flexuosa</i>	v	102	83	87	57	221	194	122	239
<i>Minuartia aizoides</i>	v	141	237	213	220	63	43	88	144 **
	g	10	8	8	0	0	1	2	3
<i>Nardus stricta</i> (x10)	v	108	141	165	217 *	115	86	72	96
	g	65	46	42	54	9	5	10	12
<i>Scorzonera cana</i>	v	13	15	9	8	19	21	16	25
	g	0	1	3	0	10	4	7	5
	j	0	2	4	3	4	10	9	6
<i>Viola oreades</i>	v	18	10	1	2 ***	31	21	3	6 ***
Sum of shoots (x10)		340	398	530	626	430	330	314	451
Number of species:									
general		21	23	22	21	23	27	28	25
appearing		-	4	1	1	-	6	3	2
disappearing		-	2	2	2	-	2	2	5

species grew better in GHM and SBC than in ALH and FVG (Table 3.10).

Nardus stricta responded to transplantation to GHM very much the same as to FVG. The shoot density of *Festuca brunnescens* slightly increased in ALH, but decreased in FVG.

Agrostis vinealis possesses a great vegetative mobility and a wide ecological areal. Its shoot number increased after transplantation to every community (Tables 3.5, 3.6, 3.9). This species can be considered as a pioneer species for secondary successions in the alpine zone (see also chapter 6). *Matricaria caucasica* is another species with "ruderal" (according to GRIME 1979)

Table 3.4. Dynamics of shoots in the FVG transplanted to GHM and ALH variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

Year	FVG→GHM				FVG→ALH			
	89	90	91	92 t	89	90	91	92 t
<i>Anthoxanthum odoratum</i>	v 47	67	96	134 *	44	46	54	61
	g 3	7	9	4 *	4	7	13	5
<i>Campanula biebersteiniana</i>	v 6	15	13	15	0	0	4	1
<i>Campanula collina</i>	v 7	10	7	9	6	13	14	16
<i>Carex umbrosa</i>	v 0	0	7	13	13	1	13	15
<i>Euphrasia ossica</i>	g 0	1	0	1	0	3	2	8
<i>Festuca brunnescens</i>	v 99	104	216	200	58	58	60	87 ***
	g 25	5	40	4 ***	3	4	15	6
<i>Festuca ovina</i>	v 78	93	80	78	47	48	127	103
<i>Festuca varia</i> (x10)	v 135	163	226	349 ***	179	200	169	171
	g 103	14	107	106	85	47	216	24 ***
<i>Gentiana djimilensis</i>	v 0	14	14	8	48	40	59	63 **
<i>Leontodon hispidus</i>	v 10	18	8	7	14	16	9	2 ***
<i>Deschampsia flexuosa</i>	v 202	426	722	772 **	180	259	243	287 *
	g 20	0	11	15	3	5	22	2
<i>Minuartia aizoides</i>	v 42	76	58	42	210	125	133	159
<i>Nardus stricta</i> (x10)	v 57	114	106	110	86	122	98	81
<i>Ranunculus oreophilus</i>	v 4	7	3	0	2	8	5	4
	j 0	1	14	16	12	7	11	10
<i>Scorzonera cana</i>	v 29	37	19	17 *	21	38	21	15
	j 0	1	7	7	9	1	30	11
<i>Viola oreades</i>	v 71	0	2	0	37	7	16	26
Sum of shoots (x10)	274	375	485	614	350	398	379	349
Number of species:								
general	23	25	25	23	21	22	23	23
appearing	-	6	2	2	-	2	2	1
disappearing	-	4	2	4	-	1	1	1

properties. It has a more strict preference to GHMs and reactions negatively to transplantation to other communities.

The floristic diversity of the investigated plots did not change significantly. It slightly diminished in control plots only due to disappearance of a few rare species (*Campanula biebersteiniana*, *Cerastium purpurascens*, *Gentiana biebersteiniana*, *Gentiana oschtenica*, *Gnaphalium supinum* and *Taraxacum confusum*). There were some changes in the floristic composition of a variant of transplantation to ALH. Such minor components, as *Minuartia recurva*,

Table 3.5. Dynamics of shoots in the GHM, in the control and transplanted to SBC variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Year	GHM-Contr.				GHM→SBC			
	89	90	91	92 t	89	90	91	92 t
<i>Agrostis vinealis</i>	v 114	90	82	144	12	24	17	36
<i>Anthoxanthum odoratum</i>	v 174	166	196	254	210	141	175	277
	g 10	11	25	10 **	3	1	3	16
<i>Campanula collina</i>	v 12	11	16	6	10	15	14	17
<i>Carex atrata</i>	v 14	19	19	24	7	10	8	16
<i>Carum meifolium</i>	v 16	26	17	7 ***	42	52	28	53
	j 0	0	0	27	25	59	74	81
<i>Festuca brunnescens</i> (x10)	v 37	67	51	63	96	99	98	130 *
	g 53	2	74	14 *	95	11	20	130
<i>Geranium gymnocaulon</i>	v 187	194	224	216	166	206	194	229 **
	g 13	33	9	0	26	7	14	4 **
<i>Hedysarum caucasicum</i>	v 43	53	15	19 ***	31	65	30	27
	g 34	0	2	4 ***	55	2	0	0
	j 12	17	35	27	49	134	57	50
<i>Leontodon hispidus</i>	v 0	0	0	0	15	11	8	12 *
<i>Deschampsia flexuosa</i>	v 185	363	437	341	405	206	77	191
<i>Nardus stricta</i> (x10)	v 45	98	87	105 *	75	95	87	101
<i>Phleum alpinum</i>	v 213	275	233	263	29	87	83	106
	g 12	41	18	83 **	2	9	29	49
<i>Ranunculus oreophilus</i>	j 27	18	22	15	18	31	15	6 ***
<i>Scorzonera cana</i>	v 32	49	35	15 **	44	53	45	47
	j 0	0	0	34	4	14	12	7
<i>Veronica gentianoides</i>	v 25	40	36	31	20	47	33	51
Sum of shoots (x10)	216	327	305	342	339	342	307	404
Number of species:								
general	23	22	20	18	26	26	25	26
appearing	-	2	1	0	-	1	1	1
disappearing	-	3	3	2	-	1	2	0

Erigeron venustus and *Luzula multiflora* had disappeared after several years, whereas young *Vaccinium vitis-idaea* and *Eritrichium caucasicum* plants were detected.

3.3.4. Transplantations of snow bed communities (SBC)

Heavy snow accumulation and a short vegetative season are typical for SBC (see chapter 1). *Sibbaldia procumbens* and *Taraxacum stevenii* are the main

Table 3.6. Dynamics of shoots in the GHM transplanted to FVG and ALH variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands, ALH = alpine lichen heaths.

Year	GHM→FVG					GHM→ALH				
		89	90	91	92 t	89	90	91	92 t	
<i>Anthemis iberica</i>	v	28	41	39	50 **	35	31	16	15 **	
<i>Anthoxanthum odoratum</i>	v	180	211	226	260 **	183	239	274	117	
<i>Campanula biebersteiniana</i>	v	9	17	20	18 **	14	13	12	16	
<i>Campanula collina</i>	v	4	17	12	15	17	27	23	28	
<i>Carex atrata</i>	v	4	11	20	20	20	18	20	27	
<i>Carum meifolium</i>	v	28	60	27	17	32	40	8	2 ***	
<i>Festuca brunnescens</i> (x10)	v	45	54	72	59 *	52	98	126	101	
	g	52	13	42	6 *	2	12	206	4 *	
<i>Festuca ovina</i>	v	30	14	55	57	57	24	227	404	
<i>Gentiana djimilensis</i>	v	9	15	30	36	28	31	57	54	
<i>Geranium gymnocaulon</i>	v	193	230	221	194	177	265	222	181	
<i>Hedysarum caucasicum</i>	v	37	65	78	76	18	25	17	22	
	g	49	3	0	0	53	0	0	9 ***	
<i>Leontodon hispidus</i>	v	5	3	0	1 ***	9	19	10	1	
<i>Deschampsia flexuosa</i>	v	150	261	397	287 *	69	103	86	71	
<i>Matricaria caucasica</i>	v	43	42	56	51	54	43	31	6 ***	
<i>Nardus stricta</i> (x10)	v	48	77	85	110	61	102	81	70	
	g	11	7	4	10	13	32	20	18	
<i>Phleum alpinum</i>	v	68	81	112	92	111	102	98	61	
	g	12	4	13	3	12	8	12	2 ***	
<i>Ranunculus oreophilus</i>	j	2	0	6	19 *	24	0	11	13 *	
<i>Scorzonera cana</i>	v	49	77	61	92 *	28	35	37	32	
<i>Veronica gentianoides</i>	v	15	32	33	36	14	25	28	20	
Sum of shoots (x10)		210	275	331	330	238	334	384	312	
Number of species:										
general		28	30	26	26	28	28	28	28	
appearing		-	5	1	2	-	2	2	2	
disappearing		-	3	5	2	-	2	2	2	

dominants. The synecological areal of the species is comparatively wide, they occur in different associations (Table 3.9). These species respond positively to transplantation to other communities (Tables 3.7 and 3.8). There seems to be a significant divergence between the auto- and synecological optima of the species. *Sibbaldia procumbens* and *Taraxacum stevenii* are suppressed by stronger competitors in meadow communities. *Sibbaldia procumbens* can

Table 3.7. Dynamics of shoots in the SBC control and transplanted in GHM variants for four experimental years.

* $p > 95\%$, ** $p > 99\%$, *** $p > 99.9\%$. SBC = snow bed communities, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows.

Year	SBC-Control				SBC→GHM				
	89	90	91	92 t	89	90	91	92 t	
<i>Agrostis vinealis</i>	v	241	199	235	301 *	164	236	243	417 ***
<i>Anthoxanthum odoratum</i>	v	39	40	46	45	3	9	8	19
<i>Carex atrata</i>	v	22	14	15	18	9	6	12	10
<i>Carex oreophila</i>	v	192	251	234	284	176	221	150	159
	g	28	28	0	1 ***	51	31	3	6 ***
<i>Catabrosella variegata</i>	v	449	471	462	557	293	433	275	398 **
	g	74	22	22	7 ***	72	24	14	5 ***
<i>Gnaphalium supinum</i>	v	109	105	112	101	146	160	124	45 **
	g	0	5	4	2	3	5	9	0
<i>Minuartia aizoides</i>	v	655	454	590	665	642	726	611	794
	g	35	10	7	15	33	3	11	8 *
<i>Nardus stricta</i> (x10)	v	52	89	74	104 *	52	150	152	223 ***
	g	13	13	4	2 ***	59	23	41	12
<i>Pedicularis nordmanniana</i>	v	36	10	11	17	4	2	2	0
	g	48	11	30	21 *	4	1	0	0
<i>Phleum alpinum</i>	v	34	37	59	64 ***	2	9	7	24
	g	1	9	4	6	1	0	2	4
<i>Sibbaldia procumbens</i>	v	725	551	555	615	443	753	562	587 *
	g	27	16	9	7	28	24	3	1 ***
<i>Taraxacum stevenii</i>	v	476	437	304	344	236	367	297	272
	g	40	33	7	23	40	43	8	25
	j	89	52	168	129	0	112	132	56
Sum of shoots (x10)		392	374	369	438	298	478	414	525
Number of species:									
general		16	17	17	16	16	18	21	22
appearing		-	2	1	0	-	4	3	1
disappearing		-	1	1	1	-	1	0	0

grow on dry meadows in the Rocky Mountains, but it responded positively to experimental snow augmentation in the absence of stronger competitors (KNIGHT et al. 1979).

The shoot density of *Gnaphalium supinum* and *Carex oreophila* decreased considerably when transplanted to GHMs or FVGs. The causes of this phenomenon may be the same as for some ALH plants (see 3.3.1): either abiotic conditions or changes in interspecific interactions.

Some SBC species (*Catabrosella variegata*, *Phleum alpinum*, *Nardus stricta*) responded positively or neutrally to transplantation to GHM and

Table 3.8. Dynamics of shoots in the SBC transplanted in FVG and ALH variants for four experimental years.

* p >95%, ** p >99%, *** p >99,9%. SBC = snow bed communities, FVG = *Festuca varia* dominated grasslands, ALH = alpine lichen heaths.

Year	SBC→FVG				SBC→ALH				
		89	90	91	92 t	89	90	91	92 t
<i>Agrostis vinealis</i>	v	221	183	157	86	194	174	182	242 **
<i>Carex oreophila</i>	v	307	283	187	273	135	166	174	179 **
	g	49	46	13	19 **	22	18	10	19
<i>Catabrosella variegata</i>	v	352	358	324	303	362	252	340	337
	g	58	5	8	4 ***	57	12	1	2 ***
<i>Gnaphalium supinum</i>	v	51	45	30	30 *	206	157	193	148
<i>Minuartia aizoides</i> (x10)	v	77	64	62	115 *	88	71	85	109
	g	27	5	31	26	61	26	11	13 ***
<i>Nardus stricta</i> (x10)	v	140	145	172	224 **	437	608	618	613 **
	g	34	11	5	3 ***	2	0	0	1
<i>Phleum alpinum</i>	v	13	16	21	22	36	35	26	19 *
<i>Sibbaldia procumbens</i>	v	729	761	561	536 *	678	966	769	885 **
	g	37	8	0	0	49	18	0	1 ***
<i>Taraxacum stevenii</i>	v	439	349	323	318 *	303	340	228	365
	g	35	39	8	13 **	49	15	0	2 ***
	j	0	92	140	132	64	121	228	107 *
Sum of shoots (x10)		462	435	422	525	369	381	383	427
Number of species:									
general		15	18	18	17	14	16	18	17
appearing		-	3	2	0	-	2	2	2
disappearing		-	0	2	1	-	0	0	3

negatively in other cases. Therefore, several types of behaviour are typical for species of this community as well as of other investigated communities.

Floristic diversity remained almost constant on the control plots and FVG plots, but it increased slightly in ALHs and GHMs (Tables 3.7 and 3.8). *Carum caucasicum*, *Erigeron uniflorus*, *Euphrasia ossica* were found after the transplantation of sods from SBC to ALH. An increase in the number of *Euphrasia ossica* was especially noticeable.

In short, the conclusion can be made that adult plant individuals from SBCs are tolerant to be able to exist under variable conditions above timberline. They are effected by changes in environmental conditions resulting in alterations of the number of their vegetative and generative shoots and reduction of generative reproduction. After the transplantation of experimental squares into other communities, a few new species were observed.

Table 3.9. Relative coefficient (K) showing changes on experimental plots and natural distribution of alpine species among studied communities. K is determined for 1989 and 1992 seasons, n.d. - no data, K=1 for control plots; Raunkiaer's class of frequency is counted as an average for large (see ch. 1) and small (0.25 sq.m, n=260) plots in different communities. It shows the natural distribution of the species among the communities.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Species name	Frequency classes				Relative coefficient (K)			
	ALH	FVG	GHM	SBC	ALH	FVG	GHM	SBC
<i>Vaccinium vitis-idaea</i>	IV	-	-	-	1.00	0.20	0.20	0.14
<i>Eritrichium caucasicum</i>	IV	I	-	-	1.00	0.52	0.11	0.37
<i>Euphrasia ossica</i>	II	I	II	-	1.00	0.09	0.36	0.08
<i>Campanula collina</i>	III	IV	I	-	1.00	1.09	1.00	0.85
<i>Gentiana djimilensis</i>	V	III	II	I	1.00	0.54	0.66	2.12
					1.22	1.00	n.d.	0.62
					3.34	6.03	1.00	n.d.
<i>Trifolium polyphyllum</i>	V	I	-	-	1.00	1.40	0.78	4.62
<i>Helictotrichon versicolor</i>	V	I	-	-	1.00	1.36	2.10	1.01
<i>Carex umbrosa</i>	V	III	I	-	1.00	1.46	2.21	1.43
+ <i>C. sempervirens</i>								
<i>Festuca ovina</i>	V	III	I	-	1.00	1.92	1.69	1.42
					1.09	1.00	0.54	0.29
<i>Antennaria dioica</i>	IV	III	I	-	1.00	1.61	1.28	1.16
<i>Nardus stricta</i>	-	V	III	III	0.49	1.00	0.99	0.43
					0.50	0.98	1.00	0.58
					0.71	0.79	1.94	1.00
<i>Festuca varia</i>	-	V	II	-	0.48	1.00	1.29	0.59
<i>Deschampsia flexuosa</i>	I	III	IV	I	2.96	1.00	6.65	2.01
					0.52	0.96	1.00	0.24
<i>Festuca brunnescens</i>	-	II	V	I	1.30	1.00	1.41	1.41
					1.21	0.77	1.00	0.89
<i>Anthoxanthum odoratum</i>	I	IV	V	II	0.49	1.00	0.98	1.40
					0.47	1.01	1.00	0.96
<i>Minuartia aizoides</i>	-	III	III	IV	0.52	1.00	0.69	1.60
					0.74	0.83	1.00	1.22
					1.01	1.51	1.21	1.00
<i>Agrostis vinealis</i>	I	I	I	I	1.76	1.50	1.00	2.27
					1.05	0.31	2.07	1.00
<i>Veronica gentianoides</i>	IV	III	III	I	0.79	1.84	1.00	2.04
<i>Scorzonera cana</i>	I	III	II	-	0.71	1.33	1.00	0.94
<i>Geranium gymnocaulon</i>	-	I	V	I	0.91	0.83	1.00	1.12
<i>Hedysarum caucasicum</i>	-	II	V	-	0.54	1.86	1.00	1.02
<i>Carum meifolium</i>	I	I	IV	II	0.13	1.05	1.00	0.96
<i>Matricaria caucasica</i>	-	I	IV	II	0.07	0.65	1.00	0.67
<i>Phleum alpinum</i>	-	I	III	II	0.33	0.77	1.00	3.25
					0.23	0.85	4.67	1.00
<i>Sibbaldia procumbens</i>	-	III	IV	V	1.47	0.85	1.51	1.00
<i>Taraxacum stevenii</i>	II	I	I	V	1.39	1.19	1.51	1.00
<i>Carex oreophila</i>	-	-	I	I	0.97	0.35	0.56	1.00
<i>Catabrosella variegata</i>	-	-	I	III	0.75	0.69	1.02	1.00
<i>Gnaphalium supinum</i>	-	I	III	IV	0.80	0.61	0.32	1.00

Table 3.10. Changes of morphological traits of some alpine species after transplantation in different communities (Average value (av.) and standard error (s.e.) of leaf length for *Taraxacum stevenii* and *Helictotrichon versicolor*, height of generative shoots for *Festuca varia*, height of plants for *Geranium gymnocaulon*, mm).

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

	ALH		FVG		GHM		SBC	
	av.	s.e.	av.	s.e.	av.	s.e.	av.	s.e.
<i>Festuca varia</i>	548	33.6	538	37.3	581	25.1	413	19.2
<i>Taraxacum stevenii</i>	30	0.8	47	0.9	59	1.8	53	0.9
<i>Geranium gymnocaulon</i>	70	3.9	95	5.2	149	12.2	162	7.3
<i>Helictotrichon versicolor</i>	117	5.5	150	4.4	159	7.1	105	5.7

3.3.5. Morphological changes of separate species

The value of the investigated parameters changed considerably between plots (Table 3.10). The sizes of the studied plants decreased in the following sequences:

- Helictotrichon versicolor* GHM, FVG > ALH, SBC
- Festuca varia* GHM, FVG, ALH > SBC
- Geranium gymnocaulon* SBC, GHM > FVG > ALH
- Taraxacum stevenii* GHM > SBC > FVG > ALH

The sequences show that almost all studied species were larger in meadows than in other communities. This observation supports our above mentioned conclusions about the behaviour of these species under experimental conditions. The dominants of highly productive meadows and grasslands have their optima in the same communities, but species from semiextreme conditions (ALH, SBC) often improve their growth in other communities.

Based on a study of the calcifuge-calcicole problem in alpine grasslands, GIGON (1983, 1987) concluded that "the largest proportion of species restricted to the less extreme habitats does not occur on the more extreme ones because of abiotic factors... On the other hand, the largest part of the species restricted to the more extreme habitats does not occur on the less extreme ones because of competition."(GIGON 1987, p. 241). The present results confirm his point of view.

SUMMARY

Field observations and the analysis of the results of reciprocal transplantation between four alpine communities allowed the following conclusions.

- 1) The complex vegetation of each community is rather stable and keeps its composition and structure practically unchanged for several years after having been transplanted into alien ecological conditions above timberline.
- 2) Responses of the species to transplantation are varied. As a rule, dominants of ALHs and SBCs (communities, developing under semiextreme ecological conditions) responded positively when transplanted to more productive meadows and grasslands in absence of competition with native plants. On the other hand, dominants of alpine meadows and grasslands demonstrated negative responses when transplanted to the more severe conditions of an ALH or SBC.

Some species developed best in their original communities (*Vaccinium vitis-idaea*, *Eritrichium caucasicum* in ALH, *Gnaphalium supinum* in SBC). Still, many species can grow successfully in several communities.

(ALH = alpine lichen heaths, SBC = snow bed communities)

- 3) In each case (including control squares) the introduction of new species to transplanted plots was observed. The species seemed to infiltrate the experimental plots in the form of seeds from a transplanted community situated nearby or from surrounding vegetation of the experimental area.

4. "Mass-effect" in alpine communities of the Northwestern Caucasus

Vladimir G. ONIPCHENKO and Galina A. POKARZHEVSKAYA

4.1. INTRODUCTION

Spatial heterogeneity in plant communities has several causes, e.g. environmental heterogeneity, several characteristics of plants (distribution, growth, life cycle), interactions between plants and random factors (WATT 1947, WHITTAKER 1970, RABOTNOV 1983).

Many researchers attribute the coexistence of species and their spatial pattern to environmental heterogeneity (GRUBB 1977, SOHLBERG and BLISS 1984, CHUYO 1985). If the environment is more or less homogeneous, the theory of mass effect (SHMIDA and ELLNER 1984, WILSON 1990), i.e. the pool of diaspores from neighbouring habitats supporting populations of rare species and increasing the species variety within a community, is very useful.

The direct measuring of mass effect can be a complex matter. SHMIDA and ELLNER (1984) suggested that mass effect within a community exists if a significant difference in the floristic similarity between plots is found. In this case two neighbouring plots should be more similar than two remote ones.

The proposition is presented that the idea of mass effect can be especially useful when investigating different communities situated close to each other, e.g. for high mountain communities as in the present case. There have been only few investigations of horizontal structure in alpine communities. The aim of this work is the comparison of the horizontal structure of different types of alpine communities under consideration of the mass effect hypothesis.

Acknowledgement

This work would not have been possible without help from the volunteers of the Moscow State University expedition of 1990.

We also acknowledge the help received from M. Blinnikow, who made useful comments on the text.

4.2. METHODS

4.2.1. Field methods

The investigations were carried out during the summer of 1990 at the high mountain station of Moscow State University in the Teberda reserve. Five sample areas, 25 m² each (Fig. 4.1), were laid out within each of four community types, namely alpine lichen heaths (ALH), *Festuca varia* dominated grasslands (FVG), *Geranium gymnocaulon*-*Hedysarum caucasicum* meadows (GHM) and snow bed communities (SBC). Descriptions of the studied communities are given in Chapter 1.4. The sides of the areas were oriented along the slope. Each area was divided into one hundred square plots (50x50 cm). The plots were arranged in horizontal and vertical rows. The 52 plots within the sample areas (Fig. 4.1) were checked for the presence or absence of all vascular plant species.

4.2.2. Analysis data

For the analysis of our data, the following was obtained:

1. Dependence of floristic similarity between plots on the distance between them. The coefficient of similarity (the Sorensen's coefficient) was calculated to estimate floristic similarity between each pair of plots. The distances between small plots were subdivided into 8 classes. The first class comprised plots 0.5 m apart, the second from 0.5-1 m, the third from 1-2 m, and so on. The average value of Sorensen's coefficient was calculated for each class of distance. The correlation between the average similarity coefficient and the distance class is depicted in a graph.

Table 4.1. Floristic diversity of the alpine communities (average number of species on different plots) and total number of species on five sample plots.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

type of community	plot size				total number of species
	0.5 x 0.5 m		5 x 5 m		
	average	standard error	average	standard error	
SBC	11.6	0.18	23.0	0.15	31
ALH	17.8	0.43	33.0	0.47	42
GHM	17.0	0.6	41.2	2.9	66
FVG	9.2	0.7	41.2	2.2	79

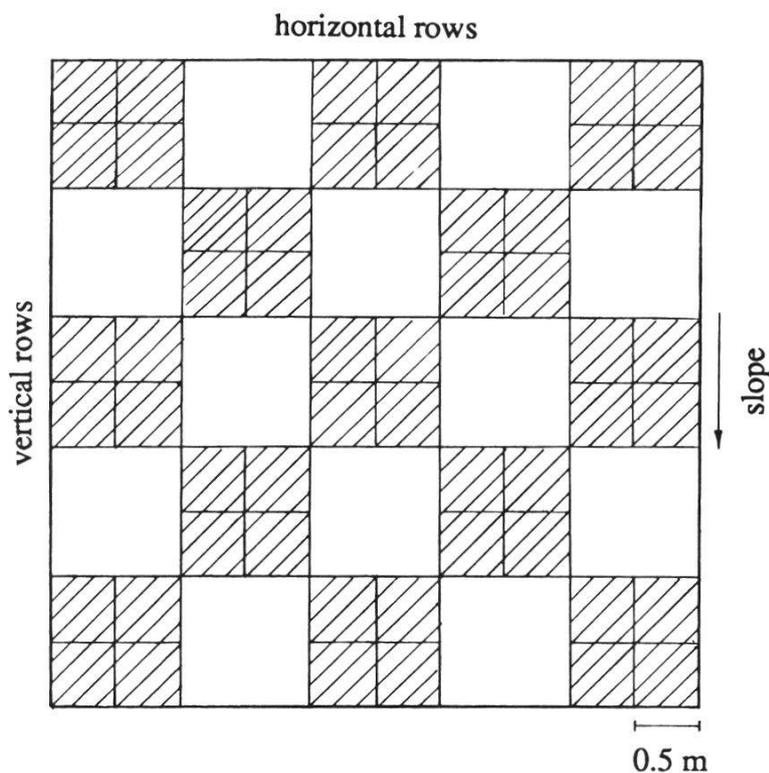


Fig. 4.1. The scheme of the sample area. Only shaded plots were studied.

2. Distribution of plant species among five Raunkiaer's frequency classes. The average frequencies of plant species was calculated for each community type.
3. Besides community structure estimations, the Euclid distance between sample areas within each community type, floristic diversity of the plots and the total number of species on the sample areas were calculated.

4.3. RESULTS

4.3.1. Floristic richness

Table 4.1 displays the floristic diversity values and the total number of species found in each community type. The poorest community type is SBC and the richest FVG. Nevertheless, for small plots, the highest number of species was found on ALHs. The same results were obtained by ONIPCHENKO and SEMENOVA (1988).

A positive correlation between the number of species and the degree of heterogeneity of community spatial structure can be expected. Then the greater the number of species the more heterogeneous the community structure will be. Thus the least heterogeneous community type should be SBC. This assumption can be compared with obtained results, shown in Fig. 4.2.

4.3.2. Degree of heterogeneity

Figure 4.2 represents the dependence of floristic similarity on the distance between plots. This dependence is different in the four studied community types. The inclination of the curve shows the degree of heterogeneity of community structure. In view of the supposed connection between the heterogeneity of structure and mass effect, the steeper the curve, the more important the mass effect is for this type of community. Thus these curves enable an estimation of the degree of mass effect.

The two-way analysis of variance has demonstrated the significant influence of the community type and the distance between plots on floristic similarity. The ALHs and SBCs have the most gently sloping curves. These types of communities are the most homogeneous of those studied, and the species of these communities are equally distributed within them. However, the SBC curve falls more rapidly than that of the ALH. We will discuss the reasons for this later.

Table 4.2. Average floristic similarity (SORENSEN's coefficient, %) between plots in vertical (v) and horizontal (h) rows of sample areas.
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

community type	row	distance between centres of plots, m						
		0.5	1.5	2.0	2.5	3.5	4.0	4.5
ALH	v	81.8	78.0	78.4	77.8	74.6	75.8	75.6
	h	79.8	78.2	77.6	76.6	77.2	75.4	74.8
FVG	v	62.4	51.2	52.0	51.0	44.6	47.4	48.2
	h	61.0	53.8	52.2	51.2	45.2	48.0	51.6
GHM	v	73.2	67.0	67.0	66.0	63.8	63.2	61.6
	h	72.6	68.0	66.4	65.0	65.2	64.0	62.6
SBC	v	82.8	76.2	76.2	75.2	71.2	72.4	72.0
	h	81.6	77.4	75.6	73.2	69.4	71.4	71.4

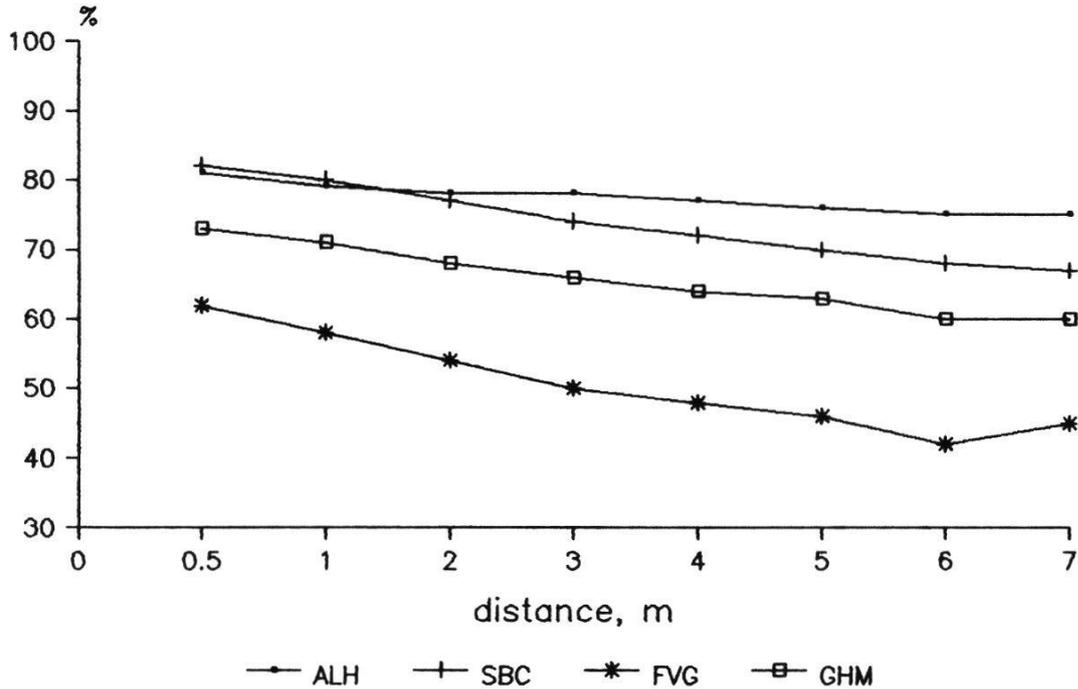


Fig. 4.2. The floristic similarity as a function of distance between plots. X-axis = distance (m) between small plots, Y-axis = average value of SORENSEN's coefficient (%). ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

The FVG possesses the steepest curve, which shows the highest level of heterogeneity of horizontal structure. The curve for GHM lies slightly higher. The results allow the conclusion, that the mass effect is most important for FVG, and least important for ALH. We can see, that these results do not precisely coincide with the assumption presented above.

4.3.3. Dependence on orientation along slope

As mentioned before, the large plots were oriented along the slope. It is suggested, that the distribution of diaspores depends on the slope processes. Then the large part of the diaspore pool will flow down the slope. Therefore, the degree of mass effect should differ in two directions; along the slope and across it.

So the comparison of floristic similarity values for vertical and horizontal rows of plots may say if mass effect depends on orientation. In this case two plots, one below the other, would have different coefficients of similarity than two plots on the same level. However, no significant differences were found

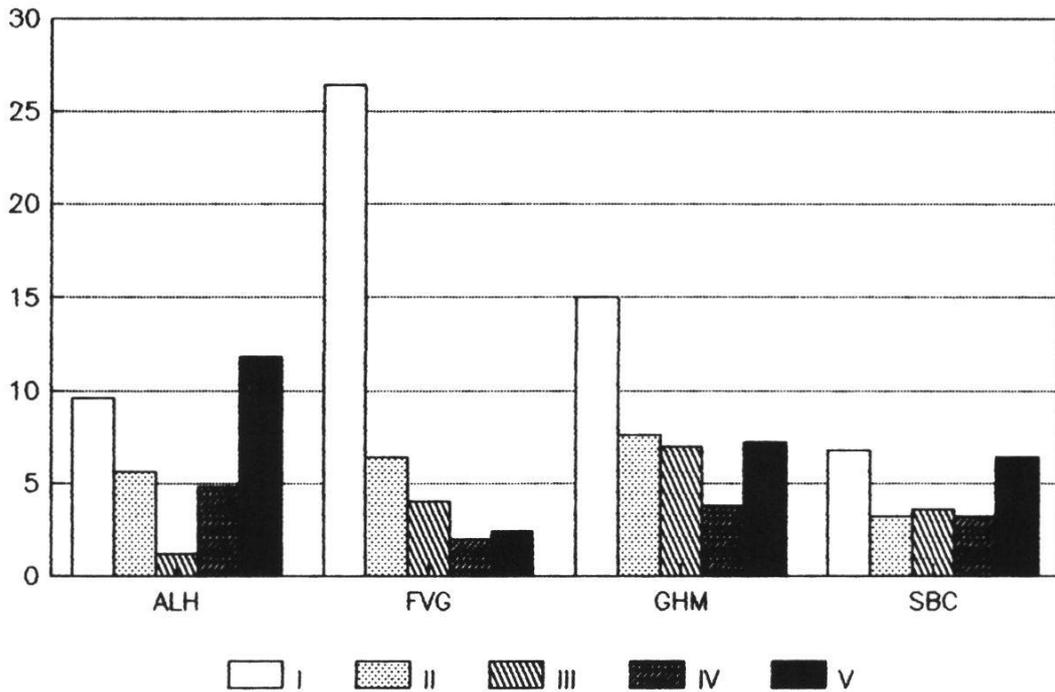


Fig. 4.3. The distribution of species among RAUNKIAER's frequency classes. Y-axis = number of species. Frequency classes of RAUNKIAER: I = 0-20%, II = 20-40%, III = 40-60%, IV = 60-80%, V = 80-100%. ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

(Tab 4.2). The obtained results are even more interesting, as the studied communities are situated on the slopes of different steepness from 1-3 up to 40 degrees.

4.3.4. Distribution among frequency classes

The studied community types have differing species distribution values among five Raunkiaers's classes of frequency (Fig. 4.3). FVGs are characterized by a low number of species with a high frequency and a considerable number of species with low frequency. SBCs and ALHs possess many species with high frequencies. Species of medium frequency (III class) are comparatively common in GHMs.

4.3.5. Results of Euclid distance calculating

An interesting body of results was obtained by the calculation of Euclid distance between sample areas within one community. It enabled the

evaluation of variation within a community. The FVGs were the least variable, which means that the sample areas were more uniform there than the plots. The similar results are found in PALMER (1990).

4.4. DISCUSSION

Based on the present research alpine community types of the Northwestern Caucasus can be characterized in the following way.

ALHs are polydominant communities, developing under the severe, snow free conditions of mountain crests (GRISHINA et al. 1986). The floristic diversity of the plots is quite high here, and there are many species with a high frequency. These communities are most homogeneous among the four studied types, and the mass effect is negligible.

The following explanation for this phenomenon is suggested: The species belonging to this community are equally distributed because the low height and only slight competitive ability of these plants set no obstacles for the settlement of the species of this community. Still, this assertion is correct perhaps only on a large scale, e.g. our sample area. In contrast, the presented data (Chapter 8) allow the statement that root competition of ALH plants can prevent other plants from growing in ALHs. Severe conditions prevent the invasion of plants from the neighbouring communities, so mass effect is negligible. There were some observations that the severe environmental conditions can be the greater on influence the establishment of seedlings than competition (see RYSER 1990).

FVGs are highly productive monodominant communities dominated by large tussocks grasses. They are the richest in species, but there are only few species with a high frequency. FVGs are the least homogeneous among the studied communities, thus the mass effect is strongly expressed there. We suppose, that the main dominants, *Festuca varia* and *Nardus stricta*, which form a tough sod, prevent other species from settling in the community. It is possible, that the input of diaspores from neighbouring communities, i.e. mass effect, can enable many species with low frequencies to survive on FVGs. These species, spreading vegetatively, form patches scattered among *Festuca* and *Nardus* tussocks. Burrowing activity of rodents and other mammals (FOMIN et al. 1989), although not very intensive here, can ease the survival of such species.

The GHM is another example of the alpine community type with a high pro-

duction and a considerable total number of species. Species with a middle frequency prevail here. Burrowing activity of animals has a great effect on this community type (FOMIN et al. 1989). The dominants, *Geranium gymnocaulon* and *Hedysarum caucasicum*, which produce a high phytomass (ONIPCHENKO 1990), may prevent settlement of other species. Although this community is rather heterogeneous, the degree of mass effect here is lower than that on FVGs. We suspect, that intensive disturbance caused by digging animals, lowers the impact of dominating species, and facilitates the settlement of the territory by other plant species. Investigations of mountain communities with differing degrees of disturbance were also conducted by LEPS and STURSA (1989). In the latter work, different results were obtained. For example, they show that the most disturbed community has the lowest number of species on small plots and the highest on large ones. Thus the authors conclude that disturbance leads to more heterogeneity, contrary to the present supposition and other works on the subject. The vegetation of SBCs must withstand a very short vegetation season (ONIPCHENKO et al. 1987). This community type is the poorest in species, yet it is less homogeneous than the ALH. This fact may be explained as caused by a slight difference in the time of snow melting during the vegetation season, which significantly effects the SBC structure.

Among other factors responsible for the heterogeneity of the community structure, the complexity of soils (OLSVIG-WHITTAKER 1988) must be mentioned. Unfortunately, no data is available at the time which takes this factor into account.

SUMMARY

Four alpine communities of the Northwestern Caucasus differ considerably from each other in the principal features of their horizontal structure.

Alpine lichen heath with predominance of fruticose lichens and snow bed communities with predominance of rosette forbs are communities which develop under severe conditions. "Mass-effect" has no great influence on the spatial structure of these phytocoenoses. The alpine grasslands are monodominant communities with predominance of large tussock plants. Here, "mass-effect" is an important factor in maintaining species diversity. The meadows take the intermediate position, in which the digging activity of animals plays a very important role, possibly decreasing that of "mass-effect" there.

The degree of mass-effect does not significantly depend on orientation to the slope. Thus, the floristic similarity/distance dependence closely corresponds to species distribution among Raunkiaer's classes of frequency. On the other hand, structural heterogeneity does not strongly depend on the number of species.

The method used in this work seems very promising and could prove a useful tool in the study of the spatial structure of vegetation.

5. Soil seed banks

Galina V. SEMENOVA and Vladimir G. ONIPCHENKO

5.1. INTRODUCTION

Information about alpine soil seed banks is very scarce (ARCHIBOLD 1984, MORIN and PAYETTE 1988, MCGROW and VAVREK 1989, HATT 1991), especially from the Caucasus (ZIROJAN 1988, GOGINA 1960). The main aim of the present research was to obtain comparative data on soil seed bank features of different alpine communities in Teberda State Reserve in the Northwestern Caucasus. The attempt was made to obtain several characteristics of seed banks, namely total number of germinable seeds, floristic composition and species diversity, spatial distribution, temporal pattern of germination, etc. These parameters can enable an appraisal of the restoration ability of studied communities after disturbances.

Acknowledgement

The authors thank A. Sennov, T. Pochatkova, T. Ulyanova, M. Makarov and N. Nedbaev for the manifold help in greenhouse experiments.

5.2. MATERIALS AND METHODS

Soil seed banks were studied in eight alpine plant communities: alpine lichen heaths (ALH), *Festuca varia* dominated grasslands (FVG), *Geranium-Hedysarum* dominated meadows (GHM), snow bed communities (SBC), *Rhododendron caucasicum* bush communities (RCB), alpine bogs (BOG) and open communities on dry and moist screes (DSC and MSC respectively). Their description is given in chapter 1 of this volume. The following fourteen sample areas were studied: ALH(U), ALH(L), FVG(U), FVG(L), GHM(U), GHM(L), SBC(U), SBC(L), RCB(U), RCB(L), BOG(1), BOG(2), DSC and MSC.

Ten soil samples 10x10x10 cm were taken from each sample area. Each

sample was divided into 2 cm-thick layers, air dried, packed and transported to the greenhouse of Moscow State University (Moscow). The samples from dry and moist screes were divided into 5 cm-thick layers, because soils of these habitats were very stony, complicating their division.

Dry samples were spread out on sterilized sand in the greenhouse and watered. We counted germinated seedlings and removed them after identification. The seedlings which we could not identify were planted and grown until they became identifiable.

Samples were taken in July-August, before seed-shedding but after complete seed germination. Therefore, it was attempted to examine only the persistent seed bank (FENNER 1985). Samples were taken in ALH in 1982 (RABOTNOV 1987), in FVG, GHM and SBC in 1986 and in RCB, BOG and screes in 1989. In the greenhouse experiment, the germination process was allowed to occur during 3-4 months in both spring and autumn, it was discontinued during summer and winter for three years of the study. We kept the samples frozen in winter to stimulate seed germination. EBERSOLE (1989) demonstrated that stratification of tundra soils tended to cause germination of a greater number of taxa.

Soil of FVG was collected for the second time in 1989 to test for differences in seed accumulation between *Festuca varia* sods and intersod space. Ten blocks, 10x10 cm, were cut to the depth of 5 cm from *Festuca varia* sods (five samples from each sample area), and ten blocks were similarly sampled from the intersod space.

The four studied communities (ALH, FVG, GHM and SBC) were additionally examined in field experiments. For this purpose five small plots of 500 cm² each were chosen in each study area (10 for each community type). The plots were fenced in by metallic hoops set 3-5 cm into the soil. The soil within the fence was ploughed and cleared of plants. To prevent seed loss, large roots, rhizomes and bulbs were washed in water which was then used to water corresponding plots. The plots were watered once or twice per week. To decrease seed invasion we removed all reproductive shoots closer than 0.5 m and covered the plots with a fine net. The net also protected the seedlings from strong light and prevented their being eaten by grasshoppers. Seedlings were counted every week and were removed when identifiable.

The field experiment began in early August, 1988. Observations were made till September and were continued during the next vegetation season. Unfortunately, there was no sense in continuing the experiment in subsequent years because, in spite of protection, seed invasion was considerable.

5.3. RESULTS AND DISCUSSION

5.3.1. Size of alpine seed banks

Soil seed bank composition of studied plant communities is presented in Tables 5.1 and 5.2. Results of seed bank investigations in ALH, FVG, GHM and SBC have already been published in more detail (SEMENOVA and ONIPCHENKO 1990, 1991).

The highest amount of viable seeds per m² was found in the soils of BOG (10675 seeds) and MSC (8080 seeds), and lowest in soils of FVG (1190 seeds) and ALH (350 seeds). Intermediate values were found for soils of GHM (3850 seeds), SBC (2810 seeds), DSC (2790 seeds) and RCB (1615 seeds). Thus, the number of germinable seeds in soils increases from dry to moist alpine communities.

These numbers of viable seeds are close to those reported for tundras and polar deserts in many research publications: up to 4000 in Taymyr tundras and from 300 to 700 in polar deserts (HODACHEK 1985), about 2000 in soils of dry tundra and about 150 in moist and hummock tundra in Canada (ARCHIBOLD 1984). Similar values were obtained for alpine meadows on silicate (1607-2291) and dolomite (1386-1455) in Davos, Switzerland (HATT 1991). The amount of viable seeds in different tundra communities in Alaska ranged from 70-600/m² (EBERSOLE 1989).

Much fewer seeds were found in alpine tundra soils in Quebec (Canada) (13-144) (MORIN and PAYETTE 1988). However, different methods were applied (washing off on meshes, with consequent germination and testing of viability for nongerminated seeds). ARCHIBOLD (1984) carried out a thorough study of soil seed banks of four alpine soils in the Canadian Rocky Mountains. At the timberline there were 931-1759 seeds/m², in a wet bog 10561 seeds/m², and in dry alpine meadow soil 20425 seeds/m². This data exceeds the present results by several times (except the bog), although it was obtained in early October after seed shed. Soils under *Campanula tridentata*-dominated snow bed communities in Aragaz, Armenia, contain 7600 seeds/m² (ZIROJAN 1988), still 2-3 times more than the present findings *Campanula* seeds constituted 78% of total seed bank.

The following data were obtained by means of the field method: ALH 272 seeds/m², FVG 108 seeds/m², GHM 846 seeds/m², and SBC 256 seeds/m². These numbers were several times less than the corresponding values of the greenhouse experiment (from 1.3 to 8.8 times in different communities). The

Table 5.1. Soil seed bank composition of 4 alpine community types: a comparison of greenhouse and field experiments (before and after slash respectively, seeds per m²). ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranimum gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities.

	community types			
	ALH	FVG	GHM	SBC
<i>Ajuga orientalis</i>	0/ 0	5/ 0	0/ 0	0/ 0
<i>Alchemilla caucasica</i>	4/ 12	5/ 0	0/ 0	5/ 0
<i>Anemone speciosa</i>	7/ 22	0/ 0	0/ 0	0/ 0
<i>Anthoxanthum odoratum</i>	0/ 0	20/ 6	155/ 72	5/ 0
<i>Arenaria lychnidea</i>	4/ 0	0/ 0	0/ 0	0/ 0
<i>Campanula biebersteiniana</i>	11/ 6	5/ 0	5/ 0	0/ 2
<i>Campanula collina</i>	0/ 2	0/ 0	0/ 0	0/ 0
<i>Carex atrata</i>	0/ 0	170/ 2	75/ 24	45/ 12
<i>Carex oreophila</i>	0/ 0	0/ 0	0/ 0	35/ 0
<i>Carex pyrenaica</i>	0/ 0	0/ 0	0/ 0	15/ 6
<i>Carex sempervirens</i>	7/ 14	0/ 0	0/ 0	0/ 0
<i>Carex umbrosa</i>	5/ 20	5/ 8	10/ 0	0/ 0
<i>Carum caucasicum</i>	18/ 36	0/ 0	0/ 0	0/ 0
<i>Carum meifolium</i>	0/ 0	0/ 0	0/ 24	0/ 0
<i>Catabrosella variegata</i>	0/ 0	0/ 0	0/ 0	20/ 16
<i>Cerastium purpurascens</i>	0/ 0	100/ 4	0/ 0	0/ 0
<i>Corydalis conorrhiza</i>	0/ 0	0/ 0	0/ 0	0/106
<i>Erigeron sp.</i>	0/ 0	0/ 0	0/ 0	5/ 0
<i>Erigeron uniflorus</i>	0/ 6	0/ 0	0/ 0	0/ 0
<i>Eritrichium caucasicum</i>	4/ 0	0/ 0	0/ 0	0/ 0
<i>Euphrasia ossica</i>	0/ 6	100/ 0	10/ 20	0/ 0
<i>Festuca brunnescens</i>	0/ 2	20/ 0	30/ 2	5/ 0
<i>Festuca ovina</i>	11/ 12	75/ 10	20/ 4	10/ 4
<i>Festuca varia</i>	0/ 0	5/ 0	5/ 0	0/ 0
<i>Gentiana aquatica</i>	4/ 0	0/ 0	0/ 0	0/ 0
<i>Gentiana djimilensis</i>	29/ 66	10/ 4	0/ 0	0/ 0
<i>Gentiana septemfida</i>	14/ 0	0/ 0	0/ 0	0/ 0
<i>Gentiana sp.</i>	0/ 20	120/ 0	0/ 0	0/ 0
<i>Gnaphalium supinum</i>	0/ 0	0/ 0	0/ 0	1475/ 16
<i>Helictotrichon versicolor</i>	7/ 0	0/ 0	0/ 0	0/ 0
<i>Juniperus hemisphaerica</i>	0/ 0	0/ 2	0/ 0	0/ 0
<i>Luzula multiflora</i>	0/ 0	20/ 0	1600/ 20	90/ 0
<i>Luzula spicata</i>	4/ 6	0/ 0	0/ 0	0/ 0
<i>Matricaria caucasica</i>	0/ 0	0/ 0	1190/ 200	25/ 0
<i>Minuartia aizoides</i>	0/ 0	0/ 0	5/ 0	5/ 0
<i>Minuartia recurva</i>	0/ 0	5/ 0	5/ 2	0/ 0
<i>Minuartia sp.</i>	0/ 0	5/ 0	0/ 0	0/ 0
<i>Myosotis alpestris</i>	0/ 0	15/ 2	0/ 0	0/ 0
<i>Nardus stricta</i>	0/ 0	455/ 0	210/ 10	20/ 2
<i>Oxytropis kubanensis</i>	22/ 6	0/ 0	0/ 0	0/ 0
<i>Pedicularis chroorrhyncha</i>	0/ 6	0/ 0	0/ 0	0/ 0
<i>Pedicularis nordmanniana</i>	0/ 0	0/ 0	0/ 0	0/ 8
<i>Phleum alpinum</i>	0/ 0	0/ 0	175/ 328	10/ 18
<i>Primula algida</i>	32/ 0	0/ 0	0/ 0	0/ 0
<i>Pulsatilla albana</i>	11/ 0	0/ 0	0/ 0	0/ 0
<i>Ranunculus oreophilus</i>	4/ 10	5/ 48	0/ 2	0/ 0

Table 5.1. (continued)

	ALH	community types		SBC
		FVG	GHM	
<i>Saxifraga moschata</i>	0 / 0	0 / 0	0 / 0	5 / 0
<i>Sedum tenellum</i>	0 / 0	0 / 0	35 / 80	0 / 0
<i>Senecio aurantiacus</i>	0 / 0	5 / 0	0 / 0	0 / 0
<i>Senecio</i> sp.	4 / 0	0 / 0	0 / 0	0 / 0
<i>Senecio taraxacifolius</i>	0 / 0	5 / 0	0 / 0	0 / 0
<i>Sibbaldia procumbens</i>	0 / 0	0 / 0	110 / 34	765 / 48
<i>Taraxacum stevenii</i>	0 / 4	0 / 0	0 / 0	245 / 12
<i>Trifolium polyphyllum</i>	4 / 0	0 / 0	0 / 0	0 / 0
<i>Trifolium spadiceum</i>	0 / 0	0 / 2	0 / 0	0 / 0
<i>Vaccinium vitis-idaea</i>	0 / 2	0 / 0	0 / 0	0 / 0
<i>Veronica gentianoides</i>	32 / 8	25 / 16	150 / 16	5 / 0
<i>Viola oreades</i>	0 / 0	5 / 2	0 / 0	0 / 0
<i>Ericaceae</i> (undeterm.)	0 / 0	0 / 0	10 / 0	0 / 0
Dicotyledons (undeterm.)	76 / 10	0 / 2	20 / 6	5 / 6
Monocotyledons (undeterm.)	0 / 0	5 / 0	30 / 2	15 / 0
Total number of seeds	350 / 272	1190 / 108	3850 / 846	2810 / 256
<i>Fritillaria lutea</i> (bulbs)	4 / 24	0 / 10	0 / 0	0 / 0
<i>Gagea glacialis</i> (bulbs)	0 / 0	510 / 276	2840 / 1198	990 / 404

causes of this phenomenon were discussed earlier (SEMENOVA and ONIPCHENKO 1991).

5.3.2. Seed bank composition

We determined 23 species of vascular plants in the soil seed bank of ALH, 23 species in FVG, 17 in GHM, 19 in SBC, 29 in RCB, 25 in BOG, 18 in MSC and 23 in DSC. Most of them were ordinary species of corresponding plant communities, with a few species from neighbouring plant communities. For example, such alien seeds belonged to *Pulsatilla albana* in ALH, *Saxifraga moschata* and *Veronica gentianoides* in SBC, *Sagina saginoides* in BOG, etc.

The field experiment revealed 20 species in the seed bank of ALH, twelve species in FVG, 15 species in GHM and twelve in SBC. However, the total area of soil samples here was 2.5 times more than that in the greenhouse.

There were many species which germinated in the greenhouse, but not under field conditions (Table 5.1). Most of them were rare in investigated samples, so they could be that they are absent in the samples by chance. Nevertheless,

Table 5.2. Soil seed bank composition of RCB, BOG, MSC and DSC (seeds per m²).
RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

sample areas	RCB(U)	RCB(L)	BOG(1)	BOG(2)	MSC	DSC
<i>Agrostis vinealis</i>	0	10	0	0	0	0
<i>Alchemilla caucasica</i>	0	0	0	0	0	20
<i>Alchemilla</i> sp.	30	0	0	0	0	0
<i>Alchemilla vulgaris</i> aggr.	0	0	2100	10	0	0
<i>Anemone fasciculata</i>	10	0	0	0	0	0
<i>Anemone speciosa</i>	0	0	0	0	0	10
<i>Anthoxanthum odoratum</i>	0	70	10	180	0	0
<i>Anthyllis vulneraria</i>	20	0	0	0	0	70
<i>Briza marcowiczii</i>	0	60	570	0	0	0
<i>Campanula biebersteiniana</i>	60	0	0	0	0	90
<i>Campanula ciliata</i>	0	0	0	0	0	10
<i>Campanula collina</i>	10	0	0	0	0	0
<i>Cardamine uliginosa</i>	0	0	2020	0	0	0
<i>Carex atrata</i>	80	120	20	0	150	0
<i>Carex nigra</i>	0	0	290	30	0	0
<i>Carex pyrenaica</i>	10	160	10	0	960	0
<i>Carex sempervirens</i>	0	0	0	0	0	20
<i>Carex</i> sp.	0	0	10	0	20	0
<i>Carex umbrosa</i>	0	10	0	0	0	0
<i>Carum caucasicum</i>	0	0	20	90	50	10
<i>Carum meifolium</i>	0	10	0	0	0	0
<i>Catabrosella variegata</i>	0	0	0	0	10	0
<i>Cerastium trigynum</i>	0	0	1280	6800	670	0
<i>Cirsium esculentum</i>	10	0	0	0	0	0
<i>Cirsium simplex</i>	0	0	70	0	0	0
<i>Draba hispida</i>	10	0	0	0	0	30
<i>Empetrum nigrum</i>	30	0	0	0	0	0
<i>Epilobium alpinum</i>	0	0	0	10	0	0
<i>Euphrasia ossica</i>	0	0	0	0	10	230
<i>Festuca ovina</i>	0	0	0	0	0	10
<i>Gentiana aquatica</i>	0	0	0	0	0	80
<i>Gentiana djimilensis</i>	0	0	130	470	0	80
<i>Gentiana oschtenica</i>	30	0	0	0	10	170
<i>Gentiana septemfida</i>	0	0	0	0	0	30
<i>Gnaphalium supinum</i>	20	20	0	0	0	0
<i>Hyalopoa pontica</i>	0	0	0	0	40	0
<i>Luzula multiflora</i>	130	1420	4410	760	810	0
<i>Luzula spicata</i>	0	10	0	0	60	710
<i>Matricaria caucasica</i>	0	10	0	0	0	0
<i>Minuartia aizoides</i>	0	0	70	0	0	0
<i>Minuartia circassica</i>	0	0	0	0	0	10
<i>Minuartia recurva</i>	0	0	0	0	0	10
<i>Nardus stricta</i>	0	0	30	0	0	0
<i>Oxytropis kubanensis</i>	0	10	0	10	0	0
<i>Pedicularis chroorrhyncha</i>	0	0	10	0	0	20
<i>Phleum alpinum</i>	10	220	40	0	0	0

Table 5.2. (continued)

sample areas	RCB(U)	RCB(L)	BOG(1)	BOG(2)	MSC	DSC
<i>Phryne huetii</i>	0	0	0	0	720	0
<i>Potentilla gelida</i>	0	0	0	0	0	120
<i>Primula algida</i>	30	0	0	0	0	730
<i>Primula auriculata</i>	0	0	30	10	0	0
<i>Primula ruprechtii</i>	0	0	0	0	0	20
<i>Primula meyeri</i>	10	0	0	0	70	0
<i>Rhododendron caucasicum</i>	10	30	0	0	0	0
<i>Rumex alpestris</i>	0	0	10	0	0	0
<i>Sagina saginoides</i>	0	0	1570	0	0	0
<i>Saxifraga moschata</i>	10	10	0	10	0	0
<i>Saxifraga sibirica</i>	0	0	20	30	4030	0
<i>Sedum tenellum</i>	150	140	0	10	220	10
<i>Sempervivum caucasicum</i>	0	10	0	0	0	0
<i>Sibbaldia procumbens</i>	20	40	90	20	10	0
<i>Taraxacum</i> sp.	0	0	0	0	10	0
<i>Veronica gentianoides</i>	0	0	0	0	20	130
<i>Veronica telephiiifolia</i>	0	0	0	0	140	0
Dicotyledons (undeterm.)	50	80	70	30	50	140
Monocotyledons (undeterm.)	10	0	0	0	20	0
Total number of seeds	750	2480	12880	8470	8080	2790
<i>Polygonum viviparum</i> (bulbs)	0	0	80	0	0	0
<i>Saxifraga sibirica</i> (bulbs)	0	0	20	0	160	0

seedlings of *Nardus stricta* (FVG), *Primula algida* (ALH) and *Carex oreophila* (SBC) were numerous under greenhouse conditions, but absent in the field experiment. Simultaneously there were many seedlings of *Corydalis conorhiza*, *Pedicularis nordmanniana* (SBC) and *Carum meifolium* (GHM) in the field experiment, which did not appear in the greenhouse. It seems that specific conditions are necessary for their germination.

No germinable seeds of some abundant alpine species, such as *Geranium gymnocaulon*, *Hedysarum caucasicum*, *Anthemis iberica*, *Leontodon hispidus*, *Deschampsia flexuosa*, *Antennaria dioica*, etc. were found. Most of them had comparatively high seed productivity. The following species predominated in studied seed banks:

- *Sibbaldia procumbens*, *Gnaphalium supinum*, *Taraxacum stevenii* in SBC,
- *Luzula multiflora*, *Matricaria caucasica*, *Anthoxanthum odoratum*, *Nardus stricta*, *Veronica gentianoides*, *Carex atrata* in GHM,
- *Nardus stricta*, *Carex atrata* in FVG,
- *Carum caucasicum*, *Gentiana djimilensis*, *Primula algida*, *Veronica gen-*

tianoides in ALH,

- *Cerastium trigynum*, *Briza marcowiczii*, *Carex nigra*, *Cardamine uliginosa*, *Alchemilla vulgaris* in BOG,
- *Luzula multiflora*, *Carex atrata*, *Sedum tenellum* in RBC,
- *Carex pyrenaica*, *Saxifraga sibirica*, *Cerastium trigynum*, *Luzula multiflora*, *Phryne huetii* in MSC,
- *Primula algida*, *Luzula spicata* in DSC.

Our data confirm a well-known tendency (RABOTNOV 1983) that species with violent (RAMENSKY 1938) properties, or edificators of plant communities, usually do not accumulate viable seeds in the soil. The main part of the seed bank consists of non-dominant species, which have some features of explerent strategy (*Luzula multiflora*, *Matricaria caucasica*, *Veronica gentianoides* and so on).

Most species of ALH, SBC, BOG, MSC and DSC combine, to a certain extent, both explerent and patient strategies, because they grow under abiotic stress conditions (ecotopic patients). A store of their viable seeds may be insignificant, but they retain their germinating ability for a long time (*Sibbaldia procumbens*, *Gnaphalium supinum*, *Carex atrata*). On the whole, it can be concluded that there is more correspondence between recent community composition and soil seed banks for communities developing under severe ecological conditions (ALH, DSC, MSC, BOG) than for highly productive communities (FVG, GHM, RCB).

Also it should be noted, that seeds weighing more than 4 mg are practically absent in the seed bank. At the same time, only species with seeds weighing less than 0.7 mg, are presented in the soil store by more than 100 seeds/m².

5.3.3. Species diversity

It is often believed that the floristic diversity of seed bank is considerably less than the diversity of the corresponding plant community. However, the sample areas used to estimate these parameters are usually very different, i.e. less than 1 m² in the first case and about 100 m² in the second case (RABOTNOV 1982).

The average number of plant species on 10x10 cm plots were compared with the average number of species with viable seeds in the same area (Fig. 5.1). It can be concluded, that these values are similar for FVG, GHM, SBC, RCH. The species diversity of the soil seed banks in MSC, DSC and BOG was approximately two times greater than in the present communities. These

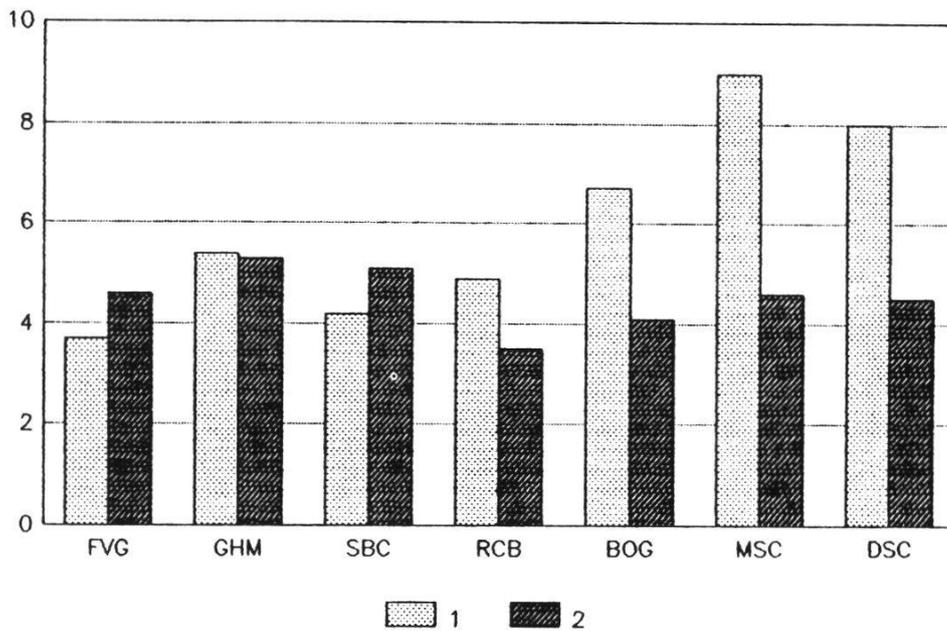


Fig. 5.1. Average number of species (floristic diversity) per 10 x 10 cm plots for soil seed banks (1) and recent plant communities (2).
 ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities. RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

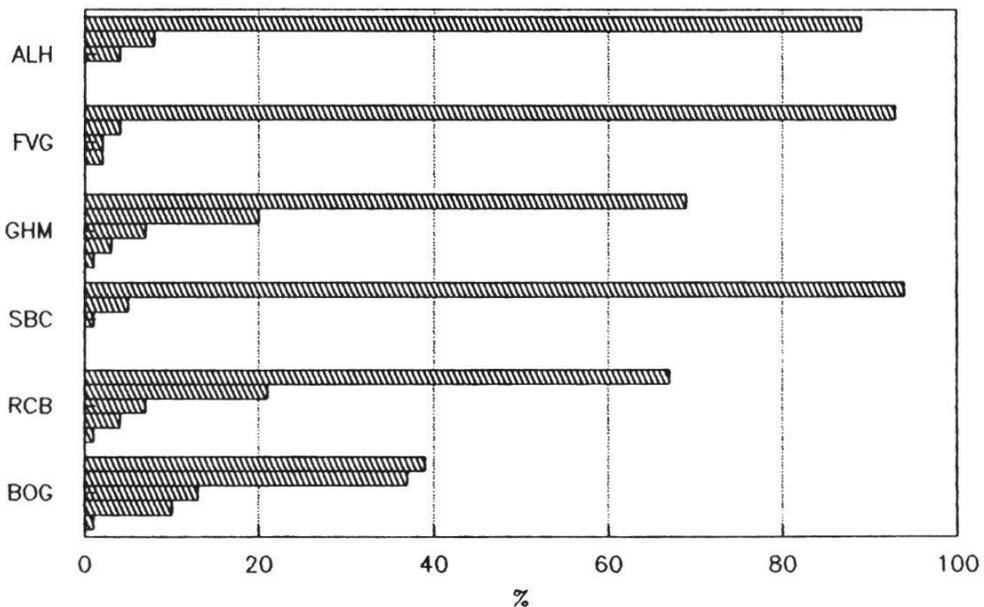


Fig. 5.2. Vertical distribution of viable seeds in 2 cm-soil layers (%) in different communities.
 ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities. RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs.

differences are reliable using the t-test. It seems that revealing of the entire species composition of a seed bank will require the investigation of larger areas than usual.

5.3.4. Spatial distribution of buried seeds

Most viable seeds are found in the upper 2 cm layer of the soil: ALH 88%, FVG 93%, GHM 70%, SBC 95%, RCB 67%, BOG 39%. Vertical distribution in soil is dissimilar in different communities (Fig. 5.2.).

Soils of DSC and MSC were divided only into two layers with 95% of the seed bank in DSC and 81% in MSC found in the upper layer (0-5 cm) of soil. Buried seeds were discovered to the depth of 10 cm of GHM, BOG and RCB soils. This is probably caused by the intensive burrowing activity of *Pitymys majori* in GHMs and submersion in peat in BOG. Viable seeds were found to the depth of 8 cm in FVG soils, less influenced by *Pitymys majori*, and to the depth of 6 cm in ALH and SBC soils, with negligible zoogenic disturbance.

Table 5.3 Soil seed bank composition of *Festuca varia* sods and intersod space in FVG (number of seeds per 10 plots with total area 0.1 sq. m)

Species	Sods	Intersod space
<i>Ajuga orientalis</i>	0	1
<i>Anthoxanthum odoratum</i>	1	0
<i>Campanula collina</i>	0	1
<i>Carex atrata</i>	27	11
<i>Cerastium purpurascens</i>	3	7
<i>Empetrum nigrum</i>	0	1
<i>Festuca</i> sp.	1	0
<i>Festuca varia</i>	3	10
<i>Gentiana djimilensis</i>	1	0
<i>Gentiana</i> sp.	0	1
<i>Luzula multiflora</i>	1	0
<i>Luzula spicata</i>	1	0
<i>Nardus stricta</i>	1	6
<i>Primula ruprechtii</i>	1	0
<i>Ranunculus oreophilus</i>	2	1
<i>Saxifraga moschata</i>	1	0
<i>Trifolium spadiceum</i>	1	0
<i>Valeriana alpestris</i>	1	0
<i>Veronica gentianoides</i>	1	1
<i>Viola oreades</i>	1	2
<i>Poaceae</i> (undeterm.)	4	0
Total number of seeds	52	42

Seeds weighing less than 0.7 mg can sink deeper into the soils than others. The lower soil layers contain mainly seeds of *Matricaria caucasica*, *Luzula multiflora*, *Nardus stricta*, *Carex atrata*, *Anthoxanthum odoratum*, *Cerastium trigynum*, *Carex pyrenaica*, *Saxifraga sibirica*.

The horizontal distribution of buried seeds is not homogeneous. The rate of heterogeneity of spatial distribution was estimated according to the variability coefficient values (CV, SD/average value). The following values were obtained for seed banks of different species: *Matricaria caucasica* 74%, *Gnaphalium supinum* 101%, *Sibbaldia procumbens* 109%, *Luzula multiflora* 113%, *Carex atrata* 110-121%, *Veronica gentianoides* 210%, *Phleum alpinum* 210%, *Taraxacum stevenii* 210%. HATT (1991) also found a significant soil bank heterogeneity for alpine meadows near Davos.

Due to a peculiar "tussock" structure of FVG, a difference in seed accumulation could be expected between *Festuca varia* sods and intersod space. However, present observations did not confirm this expectation (Table 5.3.). No significant differences in soil seed bank composition between sod and intersod samples were found. It seems that heavy accumulation of litter can even out the horizontal distribution of seeds in this community.

5.3.5. Dynamics of seed germination

The three year period of observation has allowed the estimation of the seasonal and yearly dynamics of seed germination from the soil samples (Table 5.4.). Seeds of *Nardus stricta*, *Euphrasia ossica*, *Taraxacum stevenii*, *Veronica telephiifolia* and bulbs of *Gagea glacialis* germinated only in spring. Most other seeds germinated mainly in spring. Seedlings of *Matricaria caucasica*, *Luzula multiflora*, *Carex pyrenaica*, *Phryne huetii*, *Cerastium trigynum*, *Saxifraga sibirica* and *Phleum alpinum* appeared both in spring and autumn, while seeds of *Festuca ovina* and *Festuca varia* germinated for the most part in the autumn of the first year.

Seedlings of *Nardus stricta*, *Taraxacum stevenii*, *Sedum tenellum*, *Veronica telephiifolia* and *Festuca varia* appeared only in the first year. Seeds of most alpine species germinated mainly in the first year. Seeds of *Gnaphalium supinum*, *Luzula multiflora*, *Carex atrata*, *Alchemilla vulgaris*, *Briza marcowiczii*, *Cardamine uliginosa*, *Carex nigra*, *Cerastium trigynum*, *Carex pyrenaica*, *Phryne huetii*, *Luzula spicata*, *Primula algida* and *Euphrasia ossica* germinated during all three years of the experiment. In general, from 68-96% seedlings appeared in different communities during the first year. The highest

Table 5.4. Time of seed germination of some alpine species from soil samples in the greenhouse experiment (number of seedlings for seasons and years).

FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarium caucasicum* meadows, SBC = snow bed communities, RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

Species	seasons		first	years	
	spring	autumn		second	third
FVG					
<i>Carex atrata</i>	34	0	23	3	8
<i>Cerastium purpurascens</i>	19	1	20	0	0
<i>Euphrasia ossica</i>	20	0	10	6	4
<i>Festuca ovina</i>	2	13	13	2	0
<i>Nardus stricta</i>	91	0	91	0	0
Total	219	19	193	30	15
<i>Gagea glacialis</i> (bulbs)	102	0	26	74	2
GHM					
<i>Anthoxanthum odoratum</i>	29	2	27	4	0
<i>Carex atrata</i>	14	1	10	3	2
<i>Luzula multiflora</i>	213	107	198	81	41
<i>Matricaria caucasica</i>	38	100	179	49	10
<i>Nardus stricta</i>	42	0	42	0	0
<i>Phleum alpinum</i>	16	19	34	1	0
<i>Sibbaldia procumbens</i>	21	1	19	3	0
<i>Veronica gentianoides</i>	24	6	23	7	0
Total	519	251	564	151	55
<i>Gagea glacialis</i> (bulbs)	568	0	246	212	110
SBC					
<i>Gnaphalium supinum</i>	272	23	155	97	43
<i>Luzula multiflora</i>	14	4	11	5	2
<i>Sibbaldia procumbens</i>	123	30	85	54	14
<i>Taraxacum stevenii</i>	49	0	49	0	0
Total	495	67	337	165	60
<i>Gagea glacialis</i> (bulbs)	198	0	126	41	31
RCB					
<i>Carex atrata</i>	20	0	18	2	0
<i>Carex pyrenaica</i>	13	4	11	6	0
<i>Luzula multiflora</i>	92	63	136	17	2
<i>Phleum alpinum</i>	1	22	23	0	0
<i>Sedum tenellum</i>	29	0	29	0	0
Total	227	96	284	34	5

Table 5.4. (continued)

Species	seasons		first	years	
	spring	autumn		second	third
BOG					
<i>Alchemilla vulgaris</i>	203	8	172	37	2
<i>Anthoxanthum odoratum</i>	14	5	18	1	0
<i>Briza marcowiczii</i>	44	13	44	11	2
<i>Cardamine uliginosa</i>	172	26	196	4	2
<i>Carex nigra</i>	31	1	23	7	2
<i>Cerastium trigynum</i>	267	541	787	20	1
<i>Gentiana djimilensis</i>	60	0	60	0	0
<i>Luzula multiflora</i>	383	134	371	138	8
<i>Sagina saginoides</i>	139	18	133	24	0
Total	1370	765	1862	256	17
MSC					
<i>Carex atrata</i>	15	0	11	3	1
<i>Carex pyrenaica</i>	28	68	91	4	1
<i>Cerastium trigynum</i>	25	42	65	1	1
<i>Luzula multiflora</i>	22	59	75	5	1
<i>Phryne huetii</i>	27	45	69	2	1
<i>Saxifraga sibirica</i>	44	359	398	5	0
<i>Sedum tenellum</i>	22	0	22	0	0
<i>Veronica telephiifolia</i>	14	0	14	0	0
Total	229	579	778	23	7
DSC					
<i>Euphrasia ossica</i>	23	0	16	7	0
<i>Gentiana oschtenica</i>	17	0	14	3	0
<i>Luzula spicata</i>	70	1	52	13	6
<i>Potentilla gelida</i>	12	0	8	4	0
<i>Primula algida</i>	71	2	37	23	13
<i>Veronica gentianoides</i>	13	0	7	6	0
Total	270	9	170	66	43

proportion of seeds with a late period of germination was found in SBC and DSC soils.

SUMMARY

All investigated alpine communities have a considerable stock of viable seeds in their soils. The number of seeds ranges from several hundred for ALH to more than 10'000/m² for alpine bogs. The number of germinable soil seeds tends to increase from dry to moist alpine communities.

There is more correspondence between recent community composition and soil seed banks for communities developing under severe ecological conditions (ALH, DSC, MSC, BOG) than for highly productive communities (FVG, GHM, RCB). The main dominants of alpine meadows, grasslands and bushes have few or no viable seeds in permanent seed banks. (ALH = alpine lichen heaths, DSC = open communities on dry screes, MSC = open communities on moist screes, BOG = alpine bogs, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, RCB = *Rhododendron caucasicum* bush communities).

Floristic diversity (the average number of species per dm²) is similar for recent plant communities and corresponding soil seed banks.

Most of the seeds germinated in the spring of the first year of observation. Most seeds with a late period of germination were found in SBC (snow bed communities) soils.

Two methods for studying soil seed banks are compared. The number of seedlings grown under greenhouse conditions was 1.3-8.8 times greater than those grown in the field.

6. Natural "gaps" in alpine meadows and plant population strategies

Vladimir G. ONIPCHENKO and Maria V. RABOTNOVA

6.1. INTRODUCTION

Species diversity of plant communities can be maintained by the ability of plants to occupy different regeneration niches (GRUBB 1977) according to the differing demands for seedling establishment and for development of young individuals. In the vegetation cover, disturbances create gaps of varying proportions in which different components of the plant community can be restored. This aspect of the new forest gap paradigm is widely confirmed by structural studies of different forest communities (c.f. review by PICKETT and WHITE 1985, KOROTKOV 1991). Natural disturbances are common for meadow and grassland ecosystems (COLLINS and BARBER 1986, RYSER 1990, PARISH and TURKINGTON 1990a,b). Still, the application of the regeneration niches concept in the different types of meadow communities calls for further research.

In the present paper the influence of zoogenic disturbances of differing degrees on the structure of alpine meadows is explored. The aim was to estimate the possibility of applying the "new forest gap paradigm" to alpine plant communities.

Acknowledgement

We are grateful to S. Fomin and K. Geratchenko for field assistance and to Prof. T.A. Rabotnov and M. Blinnikov for their useful comments on the earlier draft of this manuscript.

6.2. MATERIALS AND METHODS

The object of this investigation was alpine meadows with *Hedysarum caucasicum* and *Geranium gymnocaulon* as main dominants (GHM, see Chapter 1.4 for detailed description). This type of meadow is subject to the inten-

sive burrowing activity of small rodents, mainly voles *Pitymys majori* Thos. (FOMIN et al. 1989), and large mammals like wild boars (*Sus scrofa* L.) and bears (*Ursus arctos* L.). The two latter species consume the rhizome of *Hedysarum caucasicum* and other herbs. Therefore, GHMs seem very suitable for studying the influence of different scale disturbances on the composition of plant communities.

Two types of gaps were studied: 1) mesogaps (with the typical size of 1'000-10'000 cm²) formed as a result of the burrowing activity of large mammals, 2) microgaps (with the typical size of 100-1'000 cm²) formed as a result of vole's activity (Table 6.1). Mesogaps are characterized by changes in the upper soil horizon, a sharp increase in solar radiation and a considerable shift in microclimatic characteristics of the soil surface in comparison with undisturbed places. Vole burrowing also increases the availability of soil resources, slightly changing insolation of the soil surface because of shadowing by neighboring plants. In this aspect, the studied canopy gaps are analogous to different scale tree fall-out in forest plant communities (KOROTKOV 1991). Large gaps can take over 10 years to grow over, while vole burrowing places can easily recover in only a few (2-5) years. On the other hand, the latter often reappear after only a very short time.

Plots of 25x25 cm and 10x10 cm size were laid out on the disturbed places of mesogaps and microgaps respectively. The age of the studied mesogaps was about 3-5 years, and of microgaps about 1-2 years. Control plots were laid out near the gap plots on undisturbed places (not farther away than 1 m) in the same manner as the gap plots.

Table 6.1. Some features of zoogenic gaps in alpine meadows.

Burrowing mammals	mesogaps <i>Ursus arctos</i> L. <i>Sus scrofa</i> L.	microgaps <i>Pitymys majori</i> Thos.
Sizes of gaps, cm ²	1000 - 10000	100 - 1000
The periodicity of disturbances, years	> 10	1 - 8
The depth of soil disturbances, cm	5 - 20	1 - 8
Size of sample plots, cm	25 x 25	10 x 10
Number of replications (n)	270	250
Floristic diversity (number of species per plot, mean and standard error):		
gap plots	8.5 ± 1.8	5.0 ± 1.7
control plots	9.5 ± 1.3	7.3 ± 1.8

Table 6.2. Frequencies of alpine species under natural disturbances in GHM. Column "t" represents the significance level of differences according to the t-test: *** p >0.999, ** p >0.99, * p >0.95. GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows.

Species	Frequency (%)						number of group
	control	mesogaps	t	control	microgaps	t	
<i>Agrostis vinealis</i>	15.9	33.0	***	7.2	23.6	***	2
<i>Anthemis iberica</i>	17.0	37.4	***	10.0	11.2		1
<i>Anthoxanthum odoratum</i>	65.2	41.5	***	42.8	21.2	***	7
<i>Campanula biebersteiniana</i>	13.3	14.8		6.8	8.4		4
<i>Campanula collina</i>	14.8	9.6		29.2	26.4		4
<i>Carex atrata</i>	27.0	8.9	***	11.6	4.0	**	7
<i>Carum meifolium</i>	70.7	73.7		37.6	32.0		4
<i>Catabrosella variegata</i>	19.3	48.5	***	0.0	0.0		1
<i>Corydalis conorhiza</i>	47.8	34.4	**	0.0	0.0		5
<i>Daphne glomerata</i>	0.0	0.0		10.4	1.6	***	6
<i>Deschampsia flexuosa</i>	16.3	11.9		32.0	7.6	***	6
<i>Draba hispida</i>	0.0	0.0		5.2	14.4	***	3
<i>Erigeron venustus</i>	0.0	0.0		22.8	16.4		4
<i>Euphrasia ossica</i>	6.7	14.1	**	10.0	7.6		1
<i>Festuca brunnescens</i>	40.7	42.2		6.4	27.6	***	3
<i>Festuca ovina</i>	5.2	12.2	**	0.8	0.8		1
<i>Gentiana septemfida</i>	0.0	0.0		8.8	1.2	***	6
<i>Geranium gymnocaulon</i>	89.6	26.7	***	91.2	34.0	***	7
<i>Gnaphalium supinum</i>	2.2	43.7	***	0.0	0.8		1
<i>Hedysarum caucasicum</i>	47.8	34.4	**	70.4	35.6	***	7
<i>Leontodon hispidus</i>	35.2	27.8		42.4	31.2	*	6
<i>Luzula multiflora</i>	25.2	11.1	***	5.6	4.0		5
<i>Matricaria caucasica</i>	28.9	51.1	***	11.2	48.4	***	2
<i>Minuartia aizoides</i>	21.5	35.6	***	9.6	9.6		1
<i>Minuartia recurva</i>	11.9	28.1	***	8.4	4.4		1
<i>Nardus stricta</i>	42.6	15.6	***	28.8	11.2	***	7
<i>Pedicularis condensata</i>	0.0	0.0		18.8	10.8	*	6
<i>Phleum alpinum</i>	53.0	14.4	***	27.6	14.4	***	7
<i>Potentilla aurea</i>	29.6	13.0	***	5.2	4.4		5
<i>Pulsatilla aurea</i>	6.3	0.7	***	10.8	4.4	**	7
<i>Ranunculus oreophilus</i>	26.3	15.2	**	6.0	2.0	*	5
<i>Rumex alpestris</i>	43.0	10.4	***	21.2	13.6	*	7
<i>Scorzonera cana</i>	14.1	14.1		12.4	9.6		4
<i>Sedum tenellum</i>	3.3	38.1	***	1.6	5.6	*	1
<i>Senecio taraxacifolius</i>	10.0	1.1	**	0.0	0.0		5
<i>Sibbaldia procumbens</i>	24.8	48.5	***	5.6	11.6	*	2
<i>Taraxacum stevenii</i>	18.9	18.1		4.4	2.4		4
<i>Veronica gentianoides</i>	9.6	10.4		10.8	20.4	**	3

6.3. RESULTS AND DISCUSSION

Floristic diversity of control and disturbed plots did not significantly differ either in meso- or microgaps (Table 6.1). On the whole, 78 species of vascular plants were found on the plots under observation. The occurrence of the most abundant species is shown in the Table 6.2.

According to the RAMENSKY-GRIME concept, species with a positive response to disturbances belong to explerents (or ruderals) (RAMENSKY 1938, GRIME 1979, ONIPCHENKO et al. 1990).

The studied alpine species fell into the following groups, according to responses to different types of zoogenic disturbances :

1. Typical explerents. Species increasing their frequency in the mesogaps and not responding to the disturbances of a lesser scale: *Anthemis iberica*, *Catabrosella variegata*, *Euphrasia ossica*, *Festuca ovina*, *Gnaphalium supinum*, *Minuartia aizoides*, *Minuartia recurva*, *Sedum tenellum*. It seems that the development of these species is mainly determined by the increase of insolation.
2. Explerents which positively respond to different scale disturbances: *Agrostis vinealis*, *Matricaria caucasica*, *Sibbaldia procumbens*. *Agrostis vinealis* possesses the highest degree of vegetation mobility, using every possible canopy gap to form of new above-ground shoots. Other species from this group have a restricted vegetative mobility. They form a considerable soil seed bank and can rapidly resume from seeds in disturbed places (SEMENOVA and ONIPCHENKO 1990, 1991).
3. Species which increase in frequency only on microgaps and do not change (or only insignificantly) on mesogaps plots: *Draba hispida*, *Festuca brunnescens*, *Veronica gentianoides*. These species possess high tolerance to closed cover conditions and can indicate small scale disturbances.
4. Species which do not change in frequency on different scale disturbances: *Campanula biebersteiniana*, *Campanula collina*, *Carum meifolium*, *Erigeron venustus*, *Scorzonera cana*, *Taraxacum stevenii*. Most of the species have relatively large seeds and are tolerant to the wide range of ecological conditions: from open burrowing places to closed swards.
5. Species which decrease in frequency in the mesogaps and do not change (or only insignificantly) in microgaps: *Corydalis conorhiza*, *Luzula multiflora*, *Potentilla aurea*, *Ranunculus oreophilus*, *Senecio taraxacifolius*. These species adapted for growth in closed communities, but many of them can successfully resume in "small canopy breaks".

6. Species which decrease in frequency in "small canopy breaks" but do not change in mesogap plots: *Leontodon hispidus*, *Deschampsia flexuosa*. Besides these two species, *Daphne glomerata* and *Pedicularis chroorrhyncha*, not found in either mesogaps or control plots, were included in this group in advance.
7. Species which decrease in frequency both in meso and microgaps plots. This is a large group of species, which dominates or has a high frequency level in undisturbed places of the community: *Anthoxanthum odoratum*, *Carex atrata*, *Geranium gymnocaulon*, *Hedysarum caucasicum*, *Nardus stricta*, *Phleun alpinum*, *Pulsatilla aurea*, *Rumex alpestris*. Yet, most of them have comparatively large seeds and can resume under disturbances especially on microgaps. Therefore, for this group of species, natural zoenic disturbances do not cause elimination, but on the contrary can promote successful establishment of seedlings.

Based on a comparison of the amount of species with different responses to meso- and microdisturbances, it is interesting to point out that under the transition from meso- to microgaps the portion of species which responds negatively to disturbances remains invariable. The portion of species which responds positively to disturbances decreases and the portion of species indifferent to disturbances increases (Fig. 6.1).

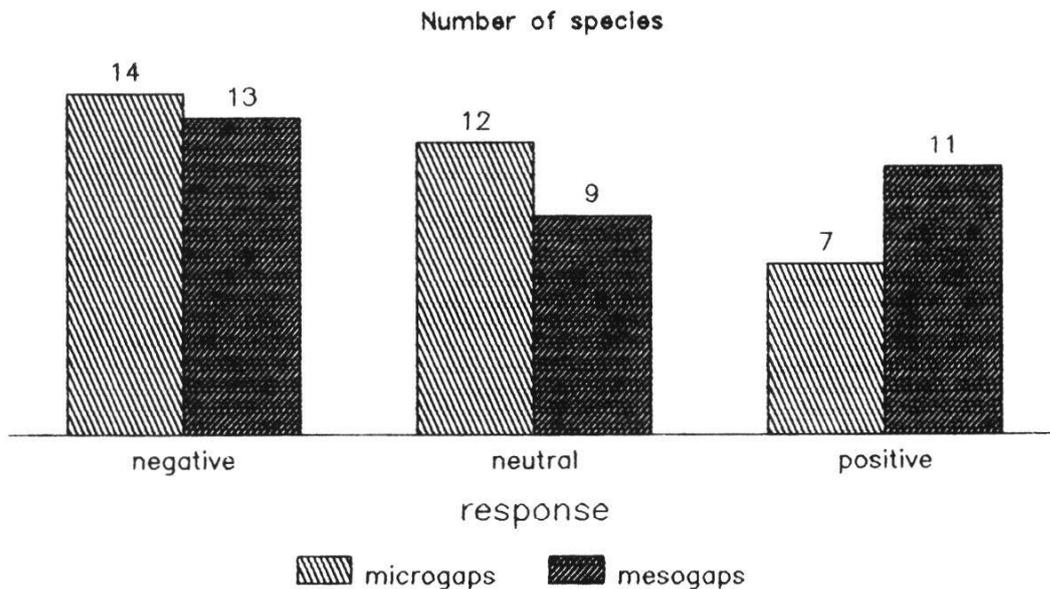


Fig. 6.1. Number of species with different responses to meso- and microdisturbances.

SUMMARY

Species occurrence on undisturbed plots and on zoogenic gaps was investigated in alpine meadow communities (GHM: = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows) in the Northwestern Caucasus. Our results lead to the conclusion that the approach of "gap-paradigm" can be fruitfully applied to the investigation of the structure of alpine plant communities.

The floristic diversity of controlled and disturbed plots did not differ significantly in either meso- or microgaps. Depending on the species responses to different types of zoogenic disturbances, the studied alpine species fell into seven groups. Reactions of alpine species to different scale disturbances are discussed using the RAMENSKY-GRIME concept. The present results agree with the classification of population strategies, developed for alpine plants of the Northwestern Caucasus (ONIPCHENKO et al. 1990).

7. Shading experiments in alpine grasslands

Vladimir G. ONIPCHENKO, Mikhail S. BLINNIKOV and Galina V. SEMENOVA

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 sustenance 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 pursued: 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.

$$K = \frac{N_{12} \times C_{11}}{N_{11} \times C_{12}}$$

N_{11} is shoot density on the experimental plots at the beginning of the experiment, N_{12} , shoot density on the experimental plots after a few years, C_{11} , shoot density on the control plots at the beginning of the experiment and C_{12} , shoot density on the control plots after the same number of years as N_{12} . 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			
	88	89	90	91
Control: no shading				
<i>Agrostis vinealis</i>	3	2	2	2
<i>Anemone speciosa</i>	1	1	1 / 1	0 / 1
<i>Antemis iberica</i>	1	1	1	2
<i>Antennaria dioica</i>	99	112 / 2	118 / 1	109
<i>Anthoxanthum odoratum</i>	58 / 1	91 / 10	128 / 9	124 / 17
<i>Campanula biebersteiniana</i>	65	90 / 1	63 / 18	55
<i>Campanula collina</i>	5	5	2	2
<i>Carex atrata</i>	1	3	2	18
<i>Carex umbrosa</i>	91 / 9	126 / 7	135 / 2	114 / 7
<i>Carum caucasicum</i>	0	4	1	0
<i>Cerastium purpurascens</i>	0	5	0	0
<i>Euphrasia ossica</i>	0 / 33	0 / 28	0 / 31	0
<i>Festuca ovina</i>	122 / 2	269 / 9	376 / 5	394 / 29
<i>Festuca varia</i>	727	853 / 40	959 / 3	990 / 37
<i>Fritillaria lutea</i>	6	0 / 1	2	0 / 1
<i>Galium verum</i>	1	1	1	2
<i>Gentiana djimilensis</i>	1	13	15	19
<i>Hedysarum caucasicum</i>	1	1	1	0
<i>Hieracium macrolepis</i>	17 / 1	11	11	8 / 1
<i>Hypericum polygonifolium</i>	3	5	1	0
<i>Nardus stricta</i>	1285 / 21	2005 / 46	2277 / 76	2259 / 127
<i>Ranunculus oreophilus</i>	2	1	0	0
<i>Scorzonera cana</i>	3	2	4	3 / 1
<i>Taraxacum stevenii</i>	0	1	0	0
<i>Veronica gentianoides</i>	6	8	6	3
<i>Viola oreades</i>	96 / 1	121 / 3	87	13
Shading for the first half of the vegetative season				
<i>Anemone speciosa</i>	0	0	1	0
<i>Antennaria dioica</i>	6	6	4	0
<i>Anthemis iberica</i>	4	4	4	5
<i>Anthoxanthum odoratum</i>	54 / 2	66 / 6	78 / 2	67 / 3
<i>Calamagrostis arundinacea</i>	114	132	112	71
<i>Campanula biebersteiniana</i>	3	2	4	2
<i>Campanula collina</i>	6 / 1	4	1 / 1	2
<i>Carex atrata</i>	0	0	2	13
<i>Carex umbrosa</i>	65	82 / 3	80 / 2	102
<i>Cerastium purpurascens</i>	2	4	1	0
<i>Deschampsia flexuosa</i>	296 / 4	436 / 8	178	27
<i>Erigeron venustus</i>	18	16	14 / 1	17 / 1
<i>Euphrasia ossica</i>	0 / 29	0 / 2	0	0
<i>Festuca ovina</i>	74 / 1	149 / 3	100 / 1	92 / 2
<i>Festuca varia</i>	760	806 / 10	562	495

Table 7.1. (continued)

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

Table 7.1. (continued)

Species	Number of shoots			
	Years			
	88	89	90	91
<i>Anthoxanthum odoratum</i>	28 / 5	29 / 3	24	11
<i>Bromopsis variegata</i>	0	0	2	0
<i>Calamagrostis arundinacea</i>	281 / 1	309 / 4	47	7
<i>Campanula collina</i>	2	1 / 1	0	0
<i>Carex atrata</i>	1	0	4	0
<i>Carex umbrosa</i>	81 / 2	95 / 4	37	6
<i>Carum caucasicum</i>	1	1	0	0
<i>Cerastium purpurascens</i>	15 / 2	11 / 6	20	9
<i>Erigeron venustus</i>	14	14	4	0
<i>Euphrasia ossica</i>	0 / 83	0 / 33	0 / 3	0
<i>Festuca ovina</i>	123 / 3	122 / 2	15	0
<i>Festuca varia</i>	361	279 / 8	73	2
<i>Fritillaria lutea</i>	2	0	3	0
<i>Gentiana djimilensis</i>	41	46 / 5	47 / 2	19
<i>Gnaphalium supinum</i>	0	0	1	0
<i>Leontodon hispidus</i>	11	8	10	0
<i>Luzula multiflora</i>	4 / 1	2 / 2	0	0
<i>Minuartia aisoides</i>	7	0	0	0
<i>Nardus stricta</i>	1288 / 35	1097 / 3	300	45
<i>Pedicularis chroorhyncha</i>	0	0	0	1
<i>Ranunculus oreophilus</i>	20 / 3	13 / 1	6	0
<i>Scorzonera cana</i>	0	0	1	0
<i>Taraxacum stevenii</i>	1	1	1	0
<i>Vaccinium vitis-idaea</i>	3	3	4	3
<i>Veronica gentianoides</i>	17	11	15	2
<i>Viola oreades</i>	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 the 1st half of the summer	22(8)	24(10)	20(6)	17(3)
	-----	-----	-----	-----
	8.3 + 1.2	8.6 + 1.3	7.0 + 1.0	5.3 + 0.8
shading for the 2nd half of the summer	21(4)	20(5)	23(4)	16(1)
	-----	-----	-----	-----
	5.9 + 1.1	5.7 + 0.9	6.3 + 1.0	4.2 + 0.7
shading for the whole summer	24(9)	21(12)	21(2)	11(0)
	-----	-----	-----	-----
	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.

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

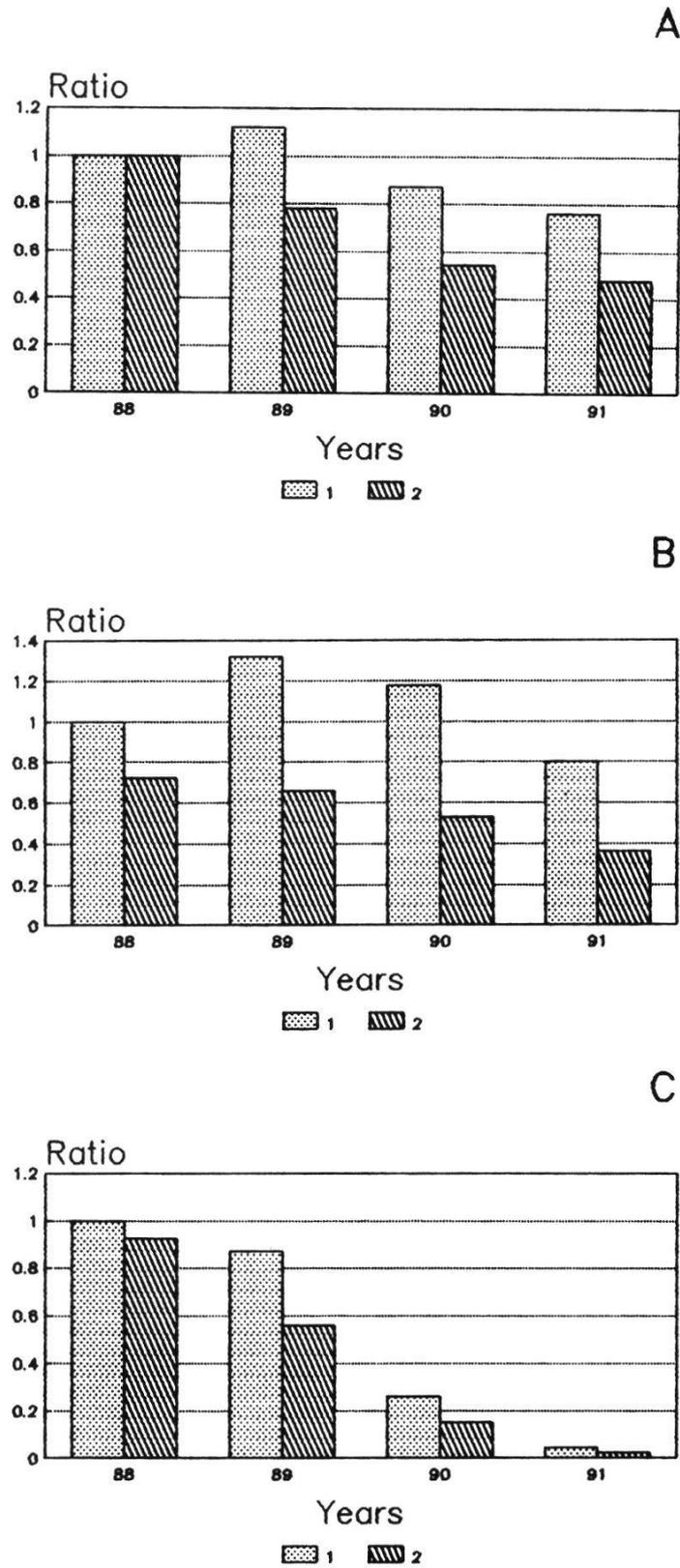


Fig. 7.1. Ratio of the total number of shoots in an experimental variant in a given year to: 1 = the total number of shoots in the variant in 1988, 2 = the total number of shoots in the control of the current year. Experimental variants: A = shading for the first half of the vegetative season, B = shading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

8. The spatial structure of alpine lichen heaths (ALH): hypothesis and experiments

Vladimir G. ONIPCHENKO

8.1. INTRODUCTION

Alpine communities with fruticose lichens as main dominants have often developed under humid conditions on windward slopes and ranges (STANJUKOVICH 1960, GORCHAKOVSKY 1975, GRABHERR et al. 1978, 1987b, WIELGOLASKI 1980, SEDELNIKOV 1988). Many of these communities have a specific fine spatial structure (GRABHERR 1987a, 1989, ONIPCHENKO 1984, 1986). ALHs belong to this type of community.

The most common pattern of spatial structure appears as small lichen areas (up to 10 cm across) alternating with graminoid bunches (*Festuca ovina*, *Carex sempervirens*, *Carex umbrosa*) or isolated shoots of vascular plants. Pure lichen or vascular plant patches with diameters of more than 20 cm do not occur in this community. There is a significant amount of thin roots in the soil under the lichen patches (Fig. 8.1). The following hypothesis is suggested as an explanation of this structure (ONIPCHENKO 1985).

ALH soils are comparatively poor and shallow (Chapter 1). Because of this, vascular plants must develop wide-spread root systems. These root systems occupy a larger area than the aboveground shoots, leaving open space in the aboveground canopy of vascular plants. Fruticose lichens can occupy these free patches because they receive their main nutrients from precipitation and atmospheric dust. The lichens constitute the main part of the aboveground phytomass, but they are not able to efficiently compete with vascular plants for nutrients. Vascular plants form the "framework" of the community. Because of frequent strong winds, fruticose lichens cannot develop without that "framework." GRABHERR (1987a, 1989) suggested a similar hypothesis for the alpine sedge meadow (*Caricetum curvulae*) structure.

Accepting this hypothesis, the following assumptions can be attempted:

1. Removal of lichens probably should not change the other components of the plant community.
2. Enrichment of soil with nutrients (fertilization) should increase above-ground vascular plant biomass and decrease lichen biomass due to the competition for light.
3. Isolation of soil areas under lichen patches from roots (root cutting) should facilitate the settlement and growth of vascular plants on these areas in comparison with unisolated (control) areas (Fig. 8.2).

To prove these assumptions, a series of experiments was carried out (see also ONIPCHENKO 1984, 1985).

Acknowledgement

The help of A. Baikalova, E. Kaverina, G. Semenova, A. Sennov and many volunteers was indispensable in the fieldwork.

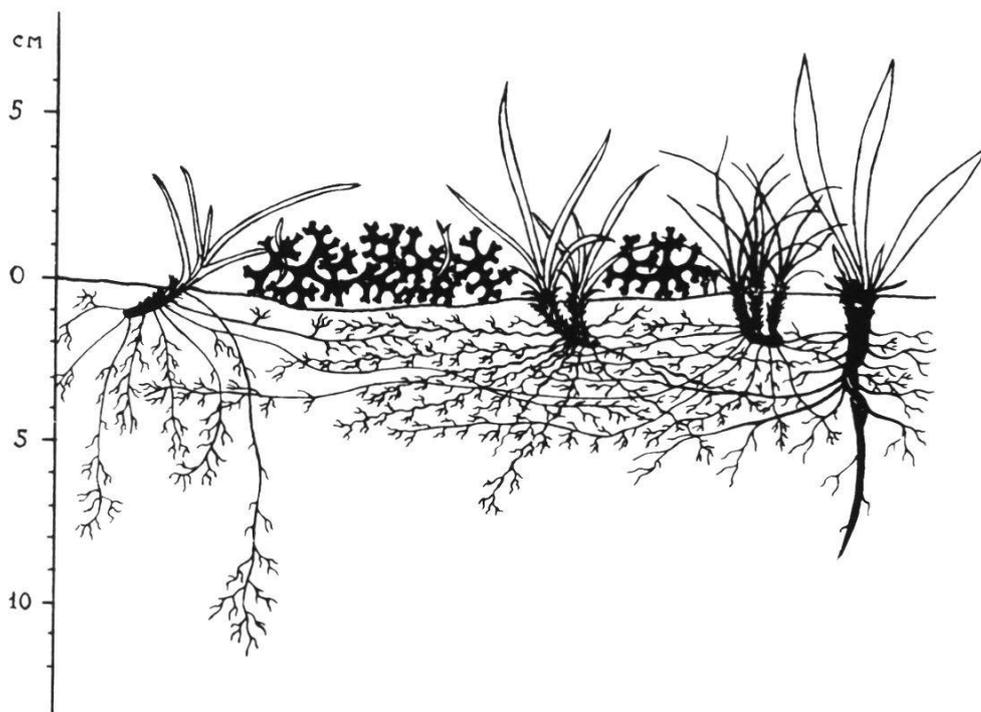


Fig. 8.1. The structure of alpine lichen heath. Plants (from left to right): *Helictotrichon versicolor*, *Cetraria islandica*, *Carex umbrosa*, *Cetraria islandica*, *Festuca ovina*, *Plantago saxatilis* (from ONIPCHENKO 1985).

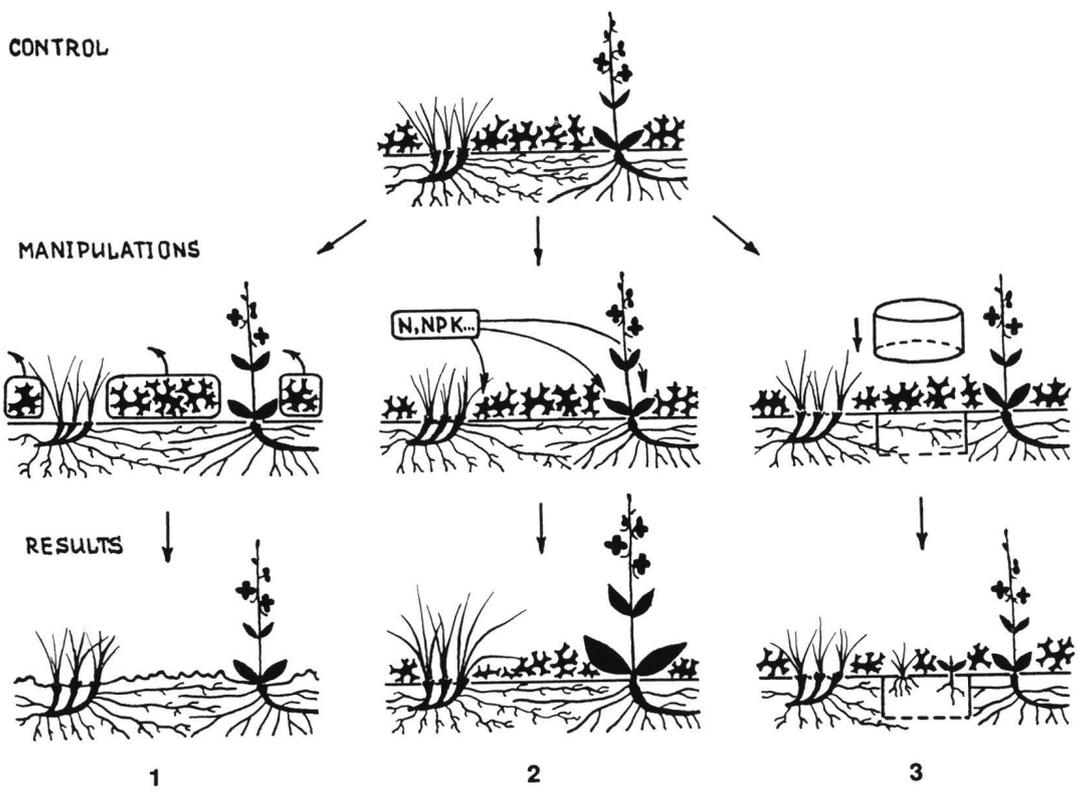


Fig. 8.2. Schematic diagram of experiments: 1 = lichen removal experiment, 2 = fertilization, 3 = root cutting.

8.2. METHODS

8.2.1. Lichen removal experiments

Four permanent plots of 1 m² size were used in the lichen removal experiment. Using pincers, fruticose lichens were carefully removed from the plots by hand. The experiment was started in August 1981. The attempt was made to remove all fruticose lichens from the experimental plots during the whole period of observation.

Shoot density was investigated on 16 small plots (25x25 cm, four plots per m²) for twelve years. The density of shoots was compared with initial data and with data from control plots.

Because of great year-to-year fluctuations of shoot density on the control and experimental plots, two methods were used to analyse the obtained data: 1) a comparison of mean shoot density on plots for the first five years of the experiment (1981-85) and for the last five years (1988-92) with t-test, 2) a calculation of a relative coefficient:

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

where N_{t1} equals shoot density on the experimental plots at the beginning of the experiment, N_{t2} , shoot density on the experimental plots after several years, C_{t1} , shoot density on the control plots at the beginning of the experiment, C_{t2} , the same for the t2 period. If $K < 1$, the shoot density of a species on experimental plots is decreasing, and if $K > 1$ it is increasing in comparison to the control (see chapter 7). K was calculated only for species with more than ten shoots per experimental and control plot. For N_{t1} and C_{t1} , mean shoot density during the first 3 experimental years (1981-83) was used and for N_{t2} and C_{t2} , the corresponding values during the three last years (1990-92).

8.2.2. Fertilization experiments

There were nine variants of the fertilization experiment: control, Ca, N, P, K, NP, NK, PK, NPK. Lime was used as a source of Ca (5 t/ha), ammonium nitrate as a source of N (90 kg N/ha), potassium chloride for K (60 kg K₂O/ha), commercial double superphosphate for P (60 kg P₂O₅/ha). Lime was applied only once (May 1981), the other fertilizers once per year of the beginning of vegetative season for three years (1981, 1982, 1983). Five plots of 2x3 m

were used for each variant. For biomass estimation, ten experimental cuts were taken at ground level from 25x25 cm plots for each variant and each year. The number of shoots was counted on each plot and the weight of single shoots was calculated. All biomass fractions had been dried at 105°C until constant weight was reached.

8.2.3. Root cutting experiments

The sod under lichen patches was isolated from neighbouring vascular plant roots by means of metallic tubes (diameter 7 or 10 cm, depth 8-10 cm, twelve replications). The tubes were left in the soil to prevent lateral root growth (Fig. 8.2). Control plots had the same size (five replications). The number of shoots and seedlings on experimental and control plots were counted at the end of the growth season for twelve years.

8.3. RESULTS AND DISCUSSION

8.3.1. Lichen removal experiments

There were no significant changes in the floristic composition of the vascular plants on the experimental plots after lichen removal (Table 8.1). A few annuals or spring geophytes, such as *Fritillaria lutea*, *Gentiana aquatica*, *Gentiana biebersteinii*, were found not every year.

Vascular plant cover on experimental and control plots was about 40% and did not change significantly after removal of lichens. Barren areas resulting from the removal of lichens did not decrease in size and they were not overgrown by other plants. Sometimes frost "boiling" occurred on these areas. A considerable cover of *Cladonia* species (primary thalli) was found on the areas after eleven years from the beginning of the experiment. Thalli were not deleted in order to avoid artificial damage to the soil. SENDSTAD (1981) reported on the considerable changes of some soil properties after artificial removal of fruticose lichens in arctic tundra at Spitsbergen. Unfortunately, the paper offers no information about vascular plant changes.

Shoot density of most species fluctuate greatly from year to year (Table 8.1). Unfortunately, there were some differences in the floristic composition between experimental and control plots. Some species that were common in experimental plots, were rare or absent in the control. The K values of only

eleven species could be calculated (Table 8.2). Among these species, *Gentiana djimilensis* and *Helictotrichon versicolor* had a considerable relative decrease in shoot density during the observation period. This can be connected with microclimatic changes or soil surface "boiling" since the fine roots of these plants are located close to the soil surface (ONIPCHENKO 1987). *Eritrichium caucasicum* and *Luzula spicata* showed a relatively positive response to lichen removal.

Shoot density of *Vaccinium vitis-idaea* increased three to five times between the first years and last years (Table 8.1). This slow-growing evergreen dwarf shrub apparently can compete with fruticose lichens for space.

Population density of the semiparasitic *Euphrasia ossica* rose sharply during the first years of the experiment. Species of *Euphrasia* reacted positively on disturbance, for example *Euphrasia minima* is a very abundant species on winter sport areas in the Alps (HOFER 1981). The species probably produce light stimulated seeds (GRIME 1981). *Euphrasia ossica* did not develop after artificial shading in ALHs (RABOTNOVA et al. 1992). It is obvious that the primary thalli of *Cladonia* negatively influenced the species during the last two years of the experiment (Table 8.1).

In spite of some changes on experimental plots after lichen removal, in the whole, the structure of the community and its floristic composition remained stable during the observation period. These results do not contradict the hypothesis discussed in the introduction.

8.3.2. Fertilization experiments

Significant changes in plant biomass and composition were found only in variants in which N was added (Fig. 8.3, 8.4). P effected plant productivity only in NP and NPK variants, that is, in the presence of N. Floristic composition did not change during three years of the experiment, but aboveground biomass increased significantly, especially of grasses and sedges.

Lichen biomass slightly decreased on variants NP and NPK, but the changes were insignificant. Vascular plants formed a dense cover on these variants. It seems that three years is too short a period for lichen cover degradation because of the slow rate of lichen decomposition in the community (VORONINA et al. 1986).

Vascular plants responded differently to the addition of nutrients. Sedges and grasses (*Carex umbrosa*, *Carex sempervirens*, *Festuca ovina*, *Helictotrichon versicolor*) increased in shoot density as well as in size and weight on

Table 8.1. Vascular plant shoot density on control plots and plots cleared of lichens during 12 years (number of shoots per sq.m).
t-test for differences between mean values for first and last 5 years intervals: *** p >0.999, ** p >0.99, * p >0.95. Shoot number for *Festuca ovina* and *Vaccinium vitis-idaea* is bound to multiply by 10.

Year of observation	81	82	83	84	85	86	87	88	89	90	91	92
experimental plots												
<i>Alchemilla caucasica</i> *	1	1	2	2	4	4	3	4	5	3	4	3
<i>Anemone speciosa</i>	48	50	49	47	46	43	50	51	47	55	57	39
<i>Antennaria dioica</i>	217	249	240	247	206	229	218	240	249	231	218	282
<i>Arenaria lychnidea</i> *	2	3	3	3	4	3	2	1	2	0	3	0
<i>Aster alpinus</i>	15	19	19	19	21	18	20	12	28	27	25	13
<i>Campanula</i>												
<i>biebersteiniana</i>	108	118	141	133	134	129	139	130	202	126	133	169
<i>Campanula collina</i>	9	23	21	26	11	13	21	26	40	30	29	22
<i>Carex sempervirens</i> + <i>C. umbrosa</i> **	358	438	447	447	488	473	468	478	625	567	548	540
<i>Carum caucasicum</i>	25	21	25	36	41	47	47	47	96	65	30	26
<i>Erigeron uniflorus</i>	9	7	11	16	11	5	5	11	11	7	9	12
<i>Eritrichium</i>												
<i>caucasicum</i> **	6	5	12	16	16	20	23	19	34	30	35	53
<i>Euphrasia ossica</i>	23	82	180	347	264	294	423	385	907	756	52	131
<i>Festuca ovina</i> (x 10) *	100	93	98	89	83	83	79	95	134	173	186	133
<i>Fritillaria lutea</i>	0	1	4	0	0	0	0	1	3	4	0	0
<i>Gentiana aquatica</i>	0	1	0	0	1	0	0	0	0	0	0	1
<i>Gentiana biebersteinii</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Gentiana djimilensis</i>	121	127	197	303	254	216	201	167	258	183	118	128
<i>Gentiana oschtenica</i>	0	0	0	0	0	0	0	0	0	0	3	5
<i>Gentiana septemfida</i>	1	1	1	1	1	1	1	1	2	1	1	1
<i>Helictotrichon</i>												
<i>versicolor</i> *	144	142	123	107	96	93	85	79	105	89	104	88
<i>Luzula spicata</i> **	12	5	13	14	14	8	14	21	24	27	24	11
<i>Minuartia circassica</i> *	66	19	102	109	122	115	120	115	144	116	138	114
<i>Pedicularis</i>												
<i>chroorrhyncha</i>	9	15	15	13	12	12	15	17	17	14	9	22
<i>Plantago saxatilis</i> ***	1	6	7	6	7	7	11	12	13	11	11	11
<i>Polygonum bistorta</i> *	2	3	5	2	2	2	2	5	6	8	6	2
<i>Potentilla gelida</i> *	27	34	49	51	37	54	44	45	60	48	54	54
<i>Primula algida</i> **	10	9	12	11	10	10	15	14	17	14	15	23
<i>Ranunculus oreophilus</i>	23	16	24	25	27	27	26	28	36	20	23	28
<i>Taraxacum stevenii</i>	3	2	6	3	4	1	3	6	4	7	6	4
<i>Trifolium polyphyllum</i> ___	4	6	5	7	6	6	6	6	6	6	6	6
<i>Vaccinium</i>												
<i>vitis-idaea</i> (x10) ***	36	32	45	54	65	72	86	102	115	139	136	159
<i>Veronica</i>												
<i>gentianoides</i> **	7	8	9	11	11	11	10	12	19	18	19	14

Table 8.1. (continued)

Year of observation	81	82	83	84	85	86	87	88	89	90	91	92
	control plots											
<i>Alchemilla caucasica</i>	2	2	2	2	2	2	3	2	2	2	2	2
<i>Anemone speciosa</i> ***	27	27	27	26	31	29	24	35	33	40	36	35
<i>Antennaria dioica</i>	2	1	2	0	0	0	1	1	1	1	1	2
<i>Campanula</i> <i>biebersteiniana</i>	279	221	266	337	320	363	222	441	313	281	398	344
<i>Carex sempervirens</i> + <i>C. umbrosa</i>	298	265	340	405	322	319	347	401	243	398	477	589
<i>Carum caasicum</i>	59	38	62	110	90	83	65	92	89	82	121	119
<i>Erigeron uniflorus</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eritrichium</i> <i>caucasicum</i> ***	37	33	43	51	46	59	39	75	68	79	81	99
<i>Festuca ovina</i> (x 10)	157	78	121	159	69	87	133	119	65	119	131	169
<i>Fritillaria lutea</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Gentiana djimilensis</i> ***	57	55	85	122	99	115	136	248	263	167	194	251
<i>Helictotrichon</i> <i>versicolor</i>	144	101	185	186	126	149	142	192	151	128	217	219
<i>Luzula spicata</i>	36	17	40	41	23	33	25	29	23	22	23	36
<i>Minuartia circassica</i> **	23	23	19	24	23	21	28	26	28	26	28	34
<i>Pedicularis caucasica</i>	0	1	1	1	2	3	1	3	3	2	3	0
<i>Pedicularis</i> <i>chroorrhyncha</i> **	1	1	1	1	0	2	5	1	6	5	3	4
<i>Ranunculus oreophilus</i>	2	0	1	8	0	3	2	0	3	0	0	4
<i>Taraxacum stevenii</i>	5	1	3	3	3	1	1	1	2	2	7	4
<i>Trifolium polyphyllum</i>	141	116	143	145	117	135	127	129	105	119	129	110
<i>Veronica gentianoides</i>	1	0	1	1	1	1	2	1	1	2	1	1

Table 8.2. Relative coefficient of shoot density variation (k) for several abundant species on plots cleared of lichen.

Species	coefficient
<i>Gentiana djimilensis</i>	0.31
<i>Helictotrichon versicolor</i>	0.52
<i>Anemone speciosa</i>	0.75
<i>Carex sempervirens</i> + <i>C. umbrosa</i>	0.82
<i>Carum caasicum</i>	0.84
<i>Campanula biebersteiniana</i>	0.87
<i>Trifolium polyphyllum</i>	1.34
<i>Festuca ovina</i>	1.44
<i>Minuartia circassica</i>	1.45
<i>Eritrichium caucasicum</i>	2.24
<i>Luzula spicata</i>	2.37

Table 8.3. Shoot density on permanent plots and average shoot biomass of some species in the fertilization experiment.

* Number of shoots per 8 permanent plots 25 x 25 cm. Abbreviations: n.d. - no data, aver. - average value, st. err. - standard error, Cont. - control.

Species	variant	number of shoots*:				shoot weight	
		vegetative		generative		(mg per 1 shoot)	
		1980	1982	1980	1982	aver.	st. err.
<i>Helictotrichon versicolor</i>	Cont.	78	60	0	1	54	5
	N	47	29	0	1	57	6
	NP	58	89	0	33	101	7
<i>Carex umbrosa</i> + <i>C. sempervirens</i>	Cont.	243	230	12	5	60	7
	N	166	276	9	14	77	7
	NP	325	588	41	79	88	8
<i>Luzula spicata</i>	Cont.	13	16	1	2	29	5
	N	9	16	1	2	29	6
	NP	25	14	3	9	98	15
<i>Anemone speciosa</i>	Cont.	10	14	6	3	266	22
	N	9	10	13	10	358	34
	NP	14	8	15	16	430	43
<i>Campanula biebersteiniana</i>	Cont.	2	3	0	1	70	8
	N	8	2	6	7	79	11
	NP	8	13	1	2	111	13
<i>Trifolium polyphyllum</i>	Cont.	269	314	0	3	73	11
	N	187	216	2	12	116	8
	NP	0	0	0	0	112	17
<i>Festuca ovina</i>	Cont.	n.d.	180	2	12	19	2
	N	n.d.	186	0	16	24	3
	NP	n.d.	489	1	258	29	2
<i>Antennaria dioica</i>	Cont.	109	95	0	0	42	4
	N	145	89	0	0	33	3
	NP	96	83	0	0	43	3

variants where N has been added (Table 8.3). Similar responses of grasses and sedges to fertilization has been observed in many experimental investigations of arctic and alpine ecosystems (McKENDRICK et al. 1980, SHATVORJAN 1981, JONASSON 1992). Most rosette forbs increased only in biomass without changing density. Such species as *Antennaria dioica* demonstrated no changes in shoot mass or density. As a consequence, a fraction of grasses and sedges in aboveground biomass was much greater in the variants with N

Table 8.4. Dynamics of the shoot number of some alpine species on experimental plots with root cutting and on control plots.

Year	81	82	83	84	85	86	87	88	89	90	91	92
control plots												
<i>Vaccinium vitis-idaea</i>	4	5	5	13	16	15	15	9	22	15	15	23
<i>Potentilla gelida</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Helictotrichon versicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Festuca ovina</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Euphrasia ossica</i>	0	0	2	4	4	11	0	1	1	0	1	1
<i>Primula algida</i>	0	0	0	0	0	0	0	0	0	0	0	0
experimental plots												
<i>Vaccinium vitis-idaea</i>	2	7	7	11	6	42	52	61	78	88	101	118
<i>Potentilla gelida</i>	2	3	4	2	3	6	5	5	6	6	6	7
<i>Helictotrichon versicolor</i>	0	1	1	2	6	5	3	1	1	3	4	4
<i>Festuca ovina</i>	0	0	0	1	3	5	4	10	11	17	32	44
<i>Euphrasia ossica</i>	0	0	9	7	1	17	14	11	13	38	3	7
<i>Primula algida</i>	0	1	3	1	5	6	4	4	4	5	7	5

addition than in the control (Fig. 8.4). It is interesting that the biomass of *Trifolium polyphyllum* (close species to *Trifolium alpinum*) increased in N variants. This species has no (or a few) nodules on the roots and uses essentially mineral nitrogen forms from the soil. So biomass of *Trifolium polyphyllum* did not increase in PK variants, which is not typical for *Fabaceae*-species (RABOTNOV 1973).

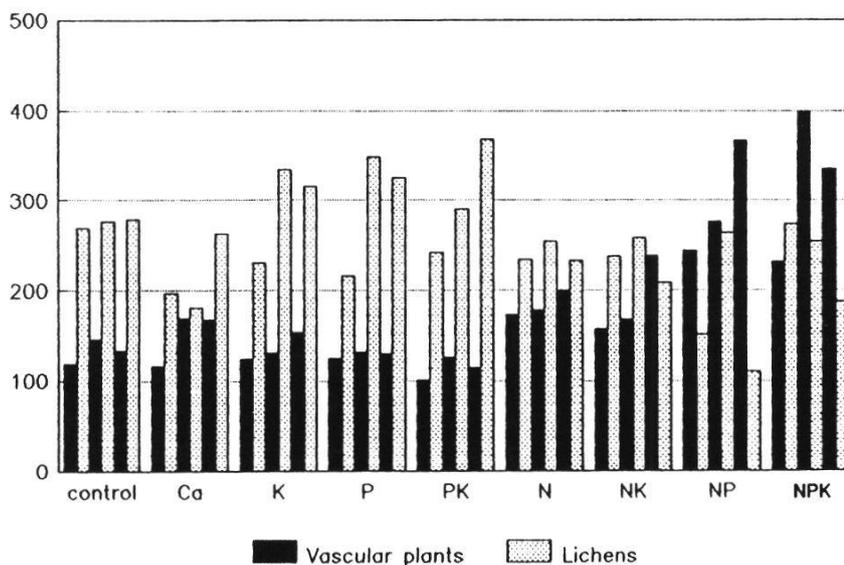


Fig. 8.3. Vascular plant and lichen biomass dynamics during 3 years of fertilization experiment. The first pair of bars in the each variant stand for 1981 values, the second for 1982 and the last for 1983 (g per m², dry mass).

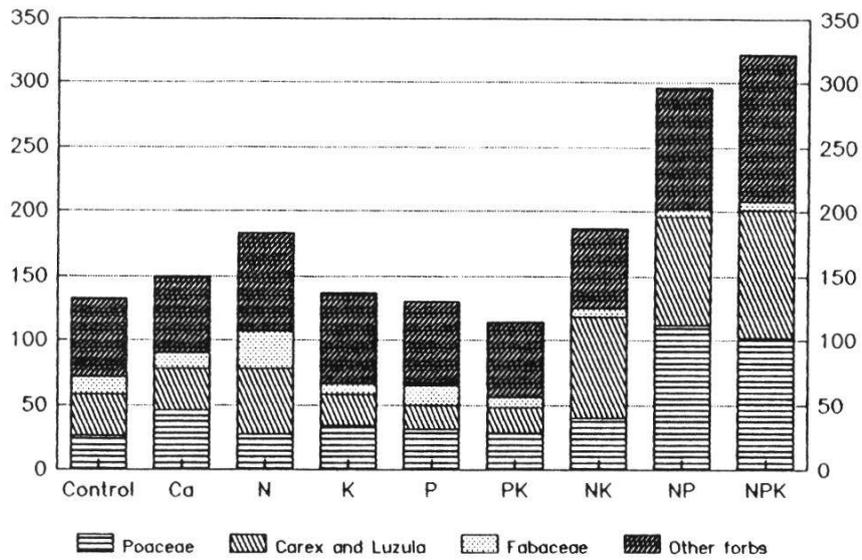


Fig. 8.4. Average vascular plant biomass composition in different variants of the fertilization experiment (g per m², dry mass).

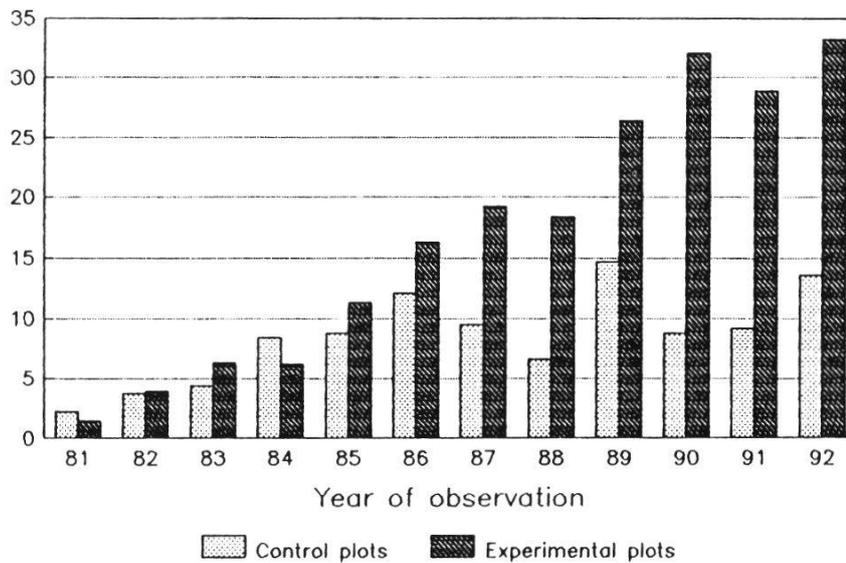


Fig. 8.5. The sum density of shoots and seedlings (average number per dm²) on experimental plots with root cutting (1) and on the control (2) for 12 years.

8.3.3. Root cutting experiments

The density of shoots and seedlings on experimental plots has slowly increased (Fig. 8.5) with some fluctuations during the observation period. Significant statistical differences to control plots was obtained only after ten years. *Vaccinium vitis-idaea*, *Festuca ovina*, *Euphrasia ossica*, *Potentilla gelida* and *Primula algida* were the most active colonists of the experi-

mental area after root cutting (Table 8.4). Most of these plants germinated from seeds originating both from soil seed bank and from recent seed rain. *Vaccinium vitis-idaea* showed no ability to form seeds in ALHs (RABOTNOV 1986), but it produces a well-developed underground shoot system for vegetative propagation. Apparently, it can develop new aboveground shoots from dormant buds after a "gap" has been detected.

SUMMARY

Alpine lichen heaths have a specific spatial structure: lichen patches alternate with graminoid bunches or isolated shoots of vascular plants. The following hypothesis was put forward as an explanation of the structure.

In poor shallow soils, the roots of vascular plants occupy a larger area than their above-ground shoots do. Thus, vacant space becomes available for fruticose lichens as there is no significant competition for nutrients with vascular plants.

It follows from this hypothesis that: 1) Removal of lichens probably should not change the other components of the plant community. 2) Enrichment of the soil with nutrients should increase above-ground plant biomass and decrease lichen biomass because of light competition. 3) Isolation of soil areas under lichen patches from roots (root cutting) should facilitate the settlement and growth of vascular plants on these areas in comparison with control areas.

To prove these hypotheses a series of long term (3-12 years) experiments was carried out. On the whole the results of these experiments conform to the hypothesis under discussion. Despite the very slow vegetative processes, which take place under severe ecological conditions at high altitudes, some of the expected results could be observed. From the results obtained it may be concluded that competition for nutrients between vascular plants plays a significant role in alpine communities, where fruticose lichens are formal dominants. It can be expected that such communities are capable of restoring themselves after slight disturbances if the sod soil level is protected. Otherwise natural process of restoration under such conditions could take many centuries.

REFERENCES

- ABDALADZE O.G., 1987: CO₂ exchange of plants in subalpine zone, the Central Caucasus (In Russ.). *Botan.Zhurn. (Soviet Journal of Botany)*, 72 (8), 1042-1049.
- AKATOV V.V., 1989: On syntaxonomy of high mountain bogs and wet meadows of the West Caucasus. (In Russ.) VINITI (Deponir. rukopis N 7472-B89), Moscow. 28 pp.
- ANDREJKO M. and COHEN A., 1984: Scanning electron microscopy of silicophytoliths from the Okefenokie swamp-march complex. In: COHEN A.D., CASAGRANDE D.L., ANDREJKO M.J. and BEST G.R. (eds.), *The Okefenokie swamp: Its natural history, geology and geochemistry. Wetland surveys, Los Alamos, New Mexico.* 468-491.
- ARCHIBOLD O.W., 1984: A comparison of seed reserves in arctic, subarctic and alpine soils. *Can.Field Natur.* 98 (3), 337-344.
- BAKER G., 1959: Opal phytoliths in some Victorian soils and "Red rain" residues. *Austr.J. Bot.* 7, 64-87.
- BLACKMAN E., 1971: Opaline silica in the range grasses of southern Alberta. *Can.J.Bot.* 49, 769-781.
- BLINNIKOV M.S., 1992: Phytolith analysis of plants and soils of alpine communities in the Northwestern Caucasus. (In Russ.) Diploma work, Geobotany Dept., Faculty of Biology, Moscow State Univ. 94 pp.
- BOUMA J., HOEKS J., VAN DER PLAS L. and VAN SCHERRENBURG B., 1969: Genesis and morphology of some Alpine Podzol Profiles. *J.Soil Sci.* 20, 384-398.
- BOUMA J. and PLAS VAN DER L., 1971: Genesis and morphology of some alpine pseudogley profiles. *J.Soil Sci.* 22, 81-93.
- BROWN D.A., 1984: Prospects and limits of a phytoliths key for grasses in the Central United States. *J.Archaeol.Sci.* 11 (4), 345-368.
- CARBONE V., 1977: Phytoliths as paleoecological indicators. *Ann. N.Y. Acad.Sci.* 288, 194-205.
- CHUYO H., 1985: Patterned grounds and vegetation in the alpine area of Mt. Ontake, central Japan. *J.Sci.Hirosima Univ., Ser.2B* 19 (2), 171-236.
- CLEMENTS F.E., 1905: *Research methods in ecology.* Univ. Publ. Co., Lincoln. 334 pp.
- CLEMENTS F.E. and HALL H.M., 1918: *Reciprocal transplantants.* Carnegie Inst.Wash. Year Book, 17, 292 pp.
- CLEMENTS F.E. and WEAVER J.E., 1924: *Experimental vegetation.* Carnegie Inst.Wash. 601 pp.
- COLLINS S.L. and BARBER S.C., 1986: Effects on disturbance on diversity in mixed-grass prairie. *Vegetatio* 64 (2-3), 87-94.
- CONNELL J.H., 1990: Apparent versus "real" competition in plants. In: GRACE J.B., TILMAN D. (ed.), *Perspectives on plant competition.* Acad.Press, San Diego. 9-26.
- COSTIN A.B., 1955: Alpine soils in Australia with reference to conditions in Europe and New Zealand. *J.Soil Sci.* 6 (1), 35-50.
- COSTIN A.B., HALLSWORTH E.G. and WOOD M., 1952: Studies in pedogenesis in New South Wales. III. The Alpine Humus Soils. *J.Soil Sci.* 3 (2), 190-218.
- DEL MORAL R., 1983: Competition as a control mechanism in subalpine meadows. *Am.J. Bot.* 70 (2), 232-245.
- DINESMAN L.G., KISELEVA N.K. and KNYASEV A.V., 1989: The history of steppe ecosystems in Mongolia [Istoriya stepnykh ekosistem MNR.]. (In Russ.). Nauka, Moscow. 214 pp.
- EBERSOLE J.J., 1989: Role of the seed bank in providing colonizers on a tundra disturbance in Alaska. *Can.J.Bot.* 67 (2), 466-471.
- ELLENBERG H., 1953: Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Ber.Deut.Bot.Ges.* 65, 351-352.
- ELLENBERG H., 1954: Über einige Fortschritte der kausalen Vegetationskunde. *Vegetatio*

5/6, 199-211.

- FENNER M., 1985: Seed ecology. Chapman and Hall, London. 160 pp.
- FOMIN S.V., ONIPCHENKO V.G. and SENNOV A.V., 1989: Feeding and digging activities of the pine vole (*Pitymys majori* Thos.) in alpine coenoses of the Northwestern Caucasus. (In Russ.) Byull. Mosk. o-va ispyt. prir. otd. biol. 94 (3), 6-13.
- GEIS J.W., 1973: Biogenetic silica in selected species of deciduous angiosperms. J.Soil Sci. 116, 113-130.
- GIGON A., 1971: Vergleich alpiner Rasen auf Silikat- und Karbonatboden. Veröff.Geobot. Inst.ETH,Stiftung Rübel, Zürich 48. 159 pp.
- GIGON A., 1983: Welches ist der wichtigste Standortsfaktor für die floristischen Unterschiede zwischen benachbarten Pflanzengesellschaften? Verh.Ges.Ökol. (Festschrift Ellenberg) 11, 145-160.
- GIGON A., 1987: A hierarchic approach in causal ecosystem analysis the calcifuge-calcicole problem in alpine grasslands. In: SCHULZE E.-D. and ZWÖLFER H. (eds.) Potentials and limitat. ecosyst. anal. (Ecol. Stud. 61). Springer, Berlin. 228-244.
- GOGINA E.E., 1960: Seed productivity of some high mountain meadow edificators in South Osetia. (In Russ.) Botan. Zhurn. 45 (9), 1330-1336.
- GORCHAKOVSKY P.L., 1975: Flora and vegetation of high mountain zone of the Ural. [Rastitelnyi mir visocogornogo Urala] (In Russ.). Nauka, Moscow. 283 pp.
- GRABHERR G., 1987a: Produktion und Produktionsstrategien im Krummseggenrasen (*Caricetum curvulae*) der Silikatalpen und ihre Bedeutung für die Bestandesstruktur. Veröff.Österr. MaB-Programm. Österr.Akad.Wiss. 10, 233-241.
- GRABHERR G., 1987b: High alpine flora and vegetation of the Tyrolean Alps (W. Austria). 14th Int.Botan.Congr. Excursion Guide (exc. 18). Berlin. 82 pp.
- GRABHERR G., 1989: On community structure in high alpine grasslands. Vegetatio 83, 223-227.
- GRABHERR G., MAHR T. and REISIGL H., 1978: Nettoprimärproduktion und Reproduktion in einem Krummseggenrasen (*Caricetum curvulae*) der Ötztaler Alpen. Tirol. Oecol. Plant. 13 (3), 227-252.
- GRACANIN Z., 1972: Die Böden der Alpen. In: GANSSEN R. and GRACANIN Z., Bodengeographie mit besonderer Berücksichtigung der Böden Mitteleuropas. Koehler, Stuttgart. 172-191.
- GRIME J.P., 1979: Plant strategies and vegetation processes. Wiley, Chichester. 222 pp.
- GRIME J.P., 1981: Plant strategies in shade. In: SMITH H. (ed), Plants and the daylight spectrum. Acad. Press, London. 159-186.
- GRISHINA L.A., CHERKINSKY A.O., ZHAKOVA O.E. and ONIPCHENKO V.G., 1987: Radiocarbon age of mountain meadow alpine soils of the Northwestern Caucasus. (In Russ.). Doklady Akademii nauk SSSR. [Reports of Soviet Acad. of Sci.] 296 (1), 218-220.
- GRISHINA L.A., ONIPCHENKO V.G., MAKAROV M.I. et al., 1986: Composition and structure of alpine heath biogeocoenosis [Sostav i struktura biogeocenočov alpijskih pustoshei] (In Russ.). Moscow Univ.Press, Moscow. 88 pp.
- GRISHINA L.A., ONIPCHENKO V.G., MAKAROV M.I. and VANJASIN V.A., 1993: The features of alpine mountain-meadow soils at different ecological conditions in the Northwestern Caucasus. Sov.Soil Sci. [Pochvovedenie] 4, 5-13.
- GROSSHEIM A.A., 1948: Vegetation of the Caucasus (In Russ.) [Rastitelnyi pokrov Kavkasa]. Mosc. Soc. Natur., New serie, 4 (XII). 268 pp.
- GRUBB P., 1977: The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol.Rev. 52 (1), 107-145.
- GUBANOV I.A., KISELEVA K.V., NOVIKOV V.S. and TIKHOMIROV V.N., 1990: Meadow plants. (In Russ.) [Lugovie travjanistye rastenia]. Agropromizdat, Moscow. 183 pp.
- HATT M., 1991: Samenvorrat von zwei alpinen Böden. Ber.Geobot.Inst.ETH, Stiftung Rübel, Zürich 57, 41-71.

- HODACHEK E.A., 1985: Soil seed banks of tundras (Taimyr) and polar deserts (Novaja Zemla). (In Russ.). *Botan. Zhurn.* 70 (7), 896-908.
- HOFER H., 1981: Der Einfluss des Massenschilauflaufes auf alpine Sauerbödenrasen am Beispiel der Gurgler Heide (Ötztal/ Tirol) und Beobachtungen zur Phänologie des *Curvuletums*. *Ber. Naturwiss.-med. Ver. Innsbruck* 68, 31-56.
- HUTCHINSON G.E., 1957: Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22, 415-422.
- JOHNSON D.D. and CLINE A.J., 1965: Colorado mountain soils. *Advances in agronomy. Acad. Press, New York and London* 17, 233-281.
- JONASSON S., 1992: Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos* 63 (3), 420-429.
- KHAPAEV S.A., 1976: Timberline oscillation in Teberda State Reserve. (In Russ.) In: AGAHANJANZ O.E. et al. (ed.) *High mountain geoecology [Vysokogornaya geoecologia.]*. *Inst. Geogr. Acad. Sci. USSR, Moscow.* 55-57.
- KISELEVA N.K., 1982: Phytolith soil studies as a tool for the investigation of the history of East Mongolia steppes. (In Russ.). *Izvestiya AN SSSR. [News of Soviet Acad. Sci.] ser. Geogr.* 2, 95-106.
- KISELEVA N.K., 1992: Botanical and phytolith analysis of Holocene zoogenic deposits in North Osetia. (In Russ.). In: DINESMAN L.G. (ed.), *Historical ecology of wild and domestic ungulates: History of pasture ecosystems. [Istoricheskaya ekologiya dikikh kopytnykh.]* Nauka, Moscow. 24-83.
- KLEIN R.L. and GEIS J.W., 1978: Biogenetic silica in the Pinaceae. *J. Soil Sci.* 126, 145-156.
- KLÖTZLI F., 1980: Zur Verpflanzung von Streu- und Moorwiesen. *ANL Tag. Ber.* 5, 41-50.
- KNIGHT D.H., WEAVER S.W., STARR C.R. and ROMME W.H., 1979: Differential response of subalpine meadow vegetation to snow augmentation. *J. Range Manag.* 32 (5), 356-359.
- KÖRNER Ch., 1982: CO₂-exchange in the alpine sedge *Carex curvula* as influenced by canopy structure, light and temperature. *Oecologia (Berlin)* 53, 98-104.
- KOROTKOV V.N., 1991: The new paradigm in forest ecology. (In Russ.). *Biol. nauki* 8, 7-20.
- LEPS J. and STURSA T., 1989: Species-area curve, life history strategies and succession: a field test of relationships. *Vegetatio* 83 (1-2), 249-257.
- LIKENS G.E. (ed.), 1989: *Long-term studies in ecology.* Springer, New York. 214 pp.
- MAKAROV M.I., 1985: Dynamics of some properties of the soils of alpine lichen heath in the Northwestern Caucasus. *Vestn. Mosk. Univ., ser. 17, 1,* 71-73.
- MAKHOVA Yu.V. and PATYK-KARA N.G., 1961: On the history of high mountain vegetation of the Great Caucasus in Holocene. (In Russ.). In: MARKOV K.K. (ed.), *Paleogeography of Quaternary period in the USSR [Paleogeographia chetvertichnogo perioda SSSR]*. Moscow. 125-130.
- MARGALITADZE N.A. and KIMERIDZE K.R., 1985: Holocene history of vegetation of Upper Svanetia. (In Russ.). In: NAKHUTSRISHVILI G.S. (ed.), *Flora and vegetation of Svanetia [Flora i rastitelnost' Svanetii]*. Mezniereba, Tbilisi. 240-260.
- MAY D.E., WEBBER P.J. and MAY T.A., 1982: Success of transplanted alpine plants on Niwot Ridge, Colorado. *Univ. Color. Inst. Arct. and Alp. Res. Occas. Pap.* 37, 73-81.
- MCGROW J.B. and VAVREK M.C., 1989: The role of buried viable seeds in arctic and alpine plant communities. In: LECK M.A. et al. (ed.), *Ecology of soil seed banks.* Acad. Press, London. 91-105.
- MCKENDRICK J.D., BATZLI G.O., EVERETT K.R. and SWANSONS J., 1980: Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct. and Alp. Res.* 12 (4), 565-578.
- MEHRA P.N. and SHARMA O.P., 1965: Epidermal silica cells in the *Cyperaceae*. *Bot. Gaz.* 126 (1), 53-58.

- METCALFE C.R., 1960: Anatomy of the Monocotyledons. I. Gramineae. Clarendon Press, Oxford. 731 pp.
- MORIN H. and PAYETTE S., 1988: Buried seed populations in the montane, subalpine, and alpine belts of Mont Jacques-Cartier, Quebec. *Can.J.Bot.* 66 (1), 101-107.
- MUELLER M., 1987: Bodenbildung auf Silikatunterlage in der alpinen Stufe des Oberengadins (Zentralalpen, Schweiz). *Catena* 14, 419-437.
- NAKHUTSRISHVILI G.S., 1974: Ecology of high-mountain plants and plant communities of the Central Caucasus. Phenology, photosynthesis and life forms. (In Russ.). [Ekologia visokogornih rastenii i fitozenosov Zentralnogo Kavkasa]. Mezniereba, Tbilisi. 194 pp.
- NAKHUTSRISHVILI G.S., 1988: Ecological characteristic of high mountain meadow vegetation (Kazbegi, Central Caucasus). (In Russ.). In: NAKHUTSRISHVILI G.Sh. (ed.), The ecology of high mountains. Mezniereba, Tbilisi. 175-200.
- NESTROY O., 1984: Aspekte der Bodenentwicklung unter Almen der Ostalpen. *Wien.Geogr.Schr.*, 59-60, 67-72.
- OLSVIG-WHITTAKER L., 1988: Relating small-scale vegetation patterns to the environment. In: DURING H.J. et al. (ed.), Diversity and pattern in plant communities. SPB Acad. Publ., Hague. 87-84.
- ONIPCHENKO V.G., 1982: The biomass of fruticose lichens in the alpine heath of the Teberdinsk Nature Reserve. (In Russ.). *Byull. Mosk. o-va ispyt.prir.otd.biol.* 87 (1), 97-99.
- ONIPCHENKO V.G., 1984: Experimental investigation of alpine lichen heath's structure. (In Russ.). *Doklady Mosk. o-va ispyt. prir. Zoologia i botanika. Nauka, Moscow.* 78-81.
- ONIPCHENKO V.G., 1985: The structure, phytomass and production of alpine lichen heaths. (In Russ.) *Byull. Mosk. o-va ispyt.prir.otd.biol.* 90 (1), 59-66.
- ONIPCHENKO V.G., 1987: Mechanisms of ecological niches separation in terrestrial plants. (In Russ.). *Zhurn. obtsh. biol. (Soviet Journal of General Biology)* 48 (5), 687-695.
- ONIPCHENKO V.G., 1990: Phytomass of the alpine communities in the Northwestern Caucasus. (In Russ.) *Byull. Mosk. o-va ispyt.prir.otd.biol.* 95 (6), 52-62.
- ONIPCHENKO V.G., GUZHOVA G.A., SEMENOVA G.V. and RABOTNOVA M.V., 1991: Population strategies of alpine plants of the Northwestern Caucasus. (In Russ.). In: SHILOV I.A. (ed.), *Ekologia populazij (Population ecology)*. Nauka, Moscow. 165-180.
- ONIPCHENKO V.G., LUBEZNOVA N.V., POKARZHEVSKAYA G.A. and RABOTNOVA M.V., 1992: Syntaxonomy of alpine plant communities in the Teberda Reserve. Class *Salicetea herbaceae* Br.-Bl. 1947. (In Russ.). *VINITI (Deponir.rukopis N 2828-B92)*, Moscow. 20 pp.
- ONIPCHENKO V.G., MINAEVA T.Y. and RABOTNOVA M.V., 1987: On syntaxonomy of alpine plant communities of Teberda reserve. (In Russ.). *VINITI (Deponir. rukopis N 1675-B87)*, Moscow. 33 pp.
- ONIPCHENKO V.G. and SEMENOVA G.V., 1988: Species richness of some alpine plant communities of the N.-W. Caucasus. *Vestn. Mosk. Univ. ser. 16 (Biol.)*, 3, 42-45.
- ONIPCHENKO V.G. and SENNOV A.V. 1992: Syntaxonomy of *Rhododendron caucasicum* - communities in the Teberda reserve (the Northwestern Caucasus). (In Russ.). *Biol. nauki* 4, 14-22.
- PALMER M.W., 1990: Spatial scale and patterns of species - environment relationships in Hardwood forest of the North Carolina Piedmont. *Coenoses* 5 (2), 79-87.
- PALMER P.G., 1976: Grass cuticles: a new paleoecological tool for East African lake sediments. *Can.J.Bot.* 54, 1725-1734.
- PARISH R. and TURKINGTON R., 1990a: The influence of dung pats and molehills on pasture composition. *Can.J.Bot.* 68 (8), 1698-1705.
- PARISH R. and TURKINGTON R., 1990b: The colonization of dung pats and molehills in permanent pastures. *Can.J.Bot.* 68 (8), 1706-1711.
- PARTRIDGE T.R. and WILSON F.B., 1988: The use of field transplants in determining envi-

- romental tolerance in salt marshes of Otago, New Zealand. *N.Z.J.Bot.* 26 (2), 183-192.
- PAVLOVA I.V. and ONIPCHENKO V.G., 1992: Holocene dynamics of the Northwestern Caucasus alpine vegetation. (In Russ.). In: DINESMAN L.G. (ed.), Historical ecology of wild and domestic ungulates: History of pasture ecosystems. [Istoricheskaja ekologija dikih i domashnih kopytnyh. Istorija pastbitznych ekosistem.]. Nauka, Moscow. 109-122.
- PICKETT S.T.A. and WHITE P.S. (ed.), 1985: The ecology of natural disturbance and patch dynamics. Acad.Press, Orlando. 472 pp.
- PIGOTT C.D., 1982: The experimental study of vegetation. *New Phytol.* 90 (3), 389-404.
- PIPERNO D.R., 1988: Phytolith analysis: An archaeological and geological perspective. Acad.Press, San Diego. 260 pp.
- PIPERNO D.R., 1991: The status of phytolith analysis in the American tropics. *J.World Prehist.* 5 (2), 155-191.
- POSCH A., 1977: Bodenkundliche Untersuchungen im Bereich der Glocknerstrasse in den Hohen Tauern (2300-2600 m MH). In: CERNUSCA A. (ed.), Alpine Grasheide Hohe Tauern. Ergebnisse der Ökosystemstudie. Innsbruck 1, 111-121.
- RABOTNOV T.A., 1982: Viable seeds in soils of natural biogeocoenoses of the USSR (In Russ.). In: DROSDOV N.N. et al. (ed.), Theoretical and applied aspects of biogeography. Nauka, Moscow. 35-59.
- RABOTNOV T.A., 1983: Phytocoenology [Phytocoenologiya]. (In Russ.). Mosc.Univ. Press, Moscow. 292 pp.
- RABOTNOV T.A. (ed.), 1987a: Biogeocoenoses of alpine heaths (NW Caucasus). (In Russ.). Nauka, Moscow. 76 pp.
- RABOTNOV T.A., 1987b: Experimental phytocoenology [Experimentalnaja phytozenologija] (In Russ.). Mosc.Univ. Press, Moscow. 160 pp.
- RABOTNOVA M.V., ONIPCHENKO V.G. and USTINOVA J.A. 1992: Influence of artificial shading on alpine lichen heaths. (In Russ. and Engl. transl.). *Vestn.Mosk.Univ.*, ser. 16 Biol., 1, 57-65.
- RAMENSKY L.G., 1938: Introduction to complex soil and geobotanical investigation of lands [Vvedenie v kompleksnoe pochveno-geobotanicheskoe izuchenie zemel] (In Russ.). Selhooziz, Moscow. 620 pp.
- RETZER J.L., 1956: Alpine soils of the Rocky Mountains. *J. Soil Sci.* 7 (1), 22-32.
- RETZER J.L., 1974: Alpine soils. In: IVES J.D. and BARRY R.G. (ed.), Arctic and alpine environments. Methuen, London. 771-802.
- ROVNER I., 1971: Potential of opal phytoliths for use in paleoecological reconstruction. *Quatern. Res.* 1, 343-359.
- RYSER P., 1990: Influence of gaps and neighbouring plants on seedling establishment in limestone grassland. *Veröff.Geobot.Inst.ETH, Stiftung Rübel, Zürich* 104. 71 pp.
- SAVINETSKY A.B., 1992: Centenary changes of pasture ecosystems in North Osetia. (In Russ.). In: DINESMAN L.G. (ed.), Historical ecology of wild and domestic ungulates: History of pasture ecosystems. [Istoricheskaja ekologija dikih i domashnih kopytnyh. Istorija pastbitznych ekosistem.]. Nauka, Moscow. 165-171.
- SEDELNIKOV V.P., 1988: High mountain vegetation of Altai and Saján mountains [Visokogornaja rastitelnoct altae-sajanskoi gornoj oblasti]. (In Russ.). Nauka, Novosibirsk. 222 pp.
- SEMENOVA G.V. and ONIPCHENKO V.G., 1990: Soil seed banks in the alpine communities in the Teberda Reserve, the Northwestern Caucasus. (In Russ.). *Byull.Mosk.o-va ispyt.prirod.biol.* 95 (5), 77-87.
- SEMENOVA G.V. and ONIPCHENKO V.G., 1991: Field investigation of the soil diasporae bank in alpine communities. (In Russ.). *Byull. Mosk.o-va ispyt.prirod.biol.* 96 (4), 117-122.
- SENDSTAD E., 1981: Soil ecology of a lichen heath at Spitsbergen, Svalbard: effects of artificial removal of the lichen plant cover. *J. Range Manag.* 34 (6), 442-445.

- SEREBRYANY L.R., GEY N.A., DZHAPARIDZE R.N. et al., 1980: Vegetation of the central part of the high mountain Caucasus in Holocene. (In Russ.). Bull. Commiss Quatern. studies [Bulletin' Comissii po izucheniyu chetvertichnogo perioda.] 50, 123-137.
- SHATVORJAN P.V., 1981: Influence of different fertilizers on production of alpine meadows with *Carum caucasicum*. (In Russ.). Armen.agricul.inst. Erevan 4, 105-111.
- SHENNIKOV A.P., 1942: Experimental view on natural factors of plant distribution. (In Russ.). Zhurn.obtch.biol. (J. Gen. Biology) 3 (5-6), 331-361.
- SHMIDA A. and ELLNER S., 1984: Coexistence of plant species with similar niches. Vegetatio 58, 29-55.
- SMITHSON F., 1958: Grass opal in British soils. J.Soil Sci. 9 (1), 148 -154.
- SOHLBERG E.H., BLISS L.C., 1984: Microscale pattern of vascular plant distribution in two high arctic plant communities. Can.J.Bot. 62 (10), 2033-2042.
- SOKOLOVA N.S., 1982: On the history of vegetation of the Great Caucasus. (In Russ.). Vestn.Mosk.Univ., ser. 5 (Geography), 5, 40-44.
- STANJUKOVICH K.B., 1960: High mountain vegetation of the USSR. [Rastitelnost visokogorii SSSR]. (In Russ.). Acad.sci. Tadjik SSR, Stalinobad. 172 pp.
- STEPANOV A.L. and ONIPCHENKO V.G., 1989: Assessment of respiration rate and nitrogen-fixing and denitrifying activity in high-meadow alpine soils of Northwestern Caucasus. Vestn.Mosk.Univ., ser. 17, 44 (2), 55-56.
- Supplement to soil classification system (7-th Approximation), 1967: Soil Survey Staff, Soil Conservation Service, U.S.D.A. 207 pp.
- SYDES C.L., GRIME J.P., 1984: A comparative study of root development using a simulated rock crevice. J.Ecol. 72 (3), 937-946.
- TAPPEINER U., CERNUSCA A. and NAKHUZRISHVILI G.S. 1989: Bestandesstruktur und Lichtklima ausgewählter Pflanzenbestände der subalpinen Stufe des Zentralkaukasus. Sitzungberichte der Österr. Akademie der Wissenschaften Mathem.-naturw. Kl., Wien, Abt.1, 197 (5-10), 395- 421.
- TILMAN D., 1988: Plant strategies and the dynamics and structure of plant communities. Monographs in population biology (v.26). Princeton Univ.Press, Princeton, New Jersey. 360 pp.
- TUSHINSKY G.K., 1962: Rythms in glaciation and snowness in Teberda State Reserve. (In Russ.). Transactions of Teberda State Reserve [Trudy Teberdinskogo Gos. Zapovednika.]. Stavropol 4, 57-71.
- TWISS P.S., SUSS E. and SMITH R.M., 1969: Morphological classification of grass phytoliths. Soil Sci.Soc.Am.Proc. 33 (1), 109-115.
- VADUNINA A.F. and KORCHAGINA Z.A., 1986: Techniques for studying of physics properties of soils. (In Russ.). Agropromizdat, Moscow. 230 pp.
- VORONINA I.N., ONIPCHENKO V.G. and IGNATOVA O.V., 1986: Components of biological turnover in alpine lichen barrens of the Northwestern Caucasus. Sov.Soil Sci. 18 (3), 20-29.
- WALTER H., HARNICKELL E. and MUELLER-DOMBOIS D. 1975: Klimadiagramm-Karten. Fischer, Stuttgart. 36 pp.
- WATT A.S., 1947: Pattern and process in the plant community. J.Ecol. 35 (1), 1-22.
- WILDING L.P., DREES L.R., 1971: Biogenetic opal in Ohio soils. Soil Sci.Soc.Am.Proc. 35, 1004 -1010.
- WILSON J.B., 1990: Mechanisms of species coexistence: twelve explanations for Hutchinson's "Paradox of the Plankton": Evidence from New Zealand plant communities. N. Z. J. Ecol. 13, 17-42.
- WIELGOLASKI F.E., 1980: Tundra plant structure and production in relation to the environment. Int.J.Biometeorol., 24 (1), 23-30.
- WITTY J.E., KNOX E.G., 1964: Grass opal in some Chestnut and Forest soils in north central Oregon. Soil Sci.Soc.Am.Proc. 28, 685 - 687.

ZINGG Th., 1961: Beitrag zum Klima vom Weissfluhjoch. Winterberg. Eidg. Inst. Schnee- und Lawinenforsch. 24, 102-127.

ZIROJAN A.N., 1988: Phytocoenotic properties and productivity of main vegetation types of Armenia. (In Russ.). Autoreferat doct. disser. Erevan. 43 pp.

ADDRESSES OF THE AUTHORS:

Mikhail S. BLINNIKOV
Vladimir G. ONIPCHENKO
Galina A. POKARZHEVSKAYA
Maria V. RABOTNOVA
Galina V. SEMENOVA
Andrej V. SENNOV

Department of Geobotany
Faculty of Biology
Moscow State University
119899 Moscow, Russia