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1. Study area and general description of the investigated communities

Vladimir G. ONIPCHENKO

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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).

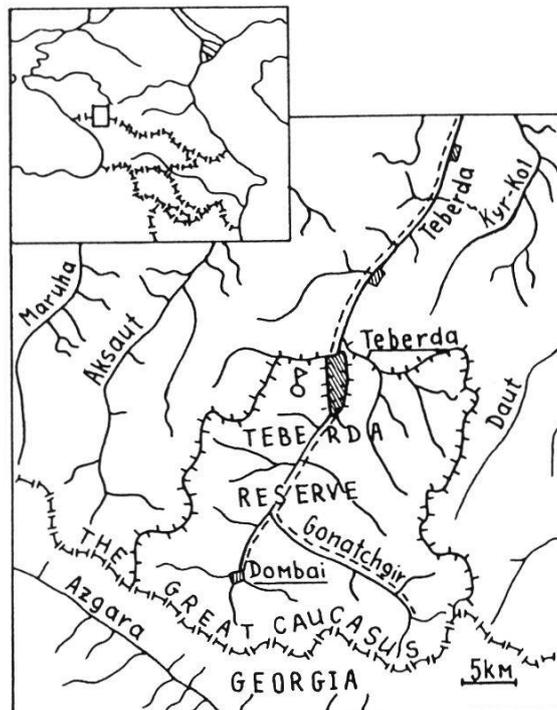


Fig. 1.1. Location of the study site.

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).

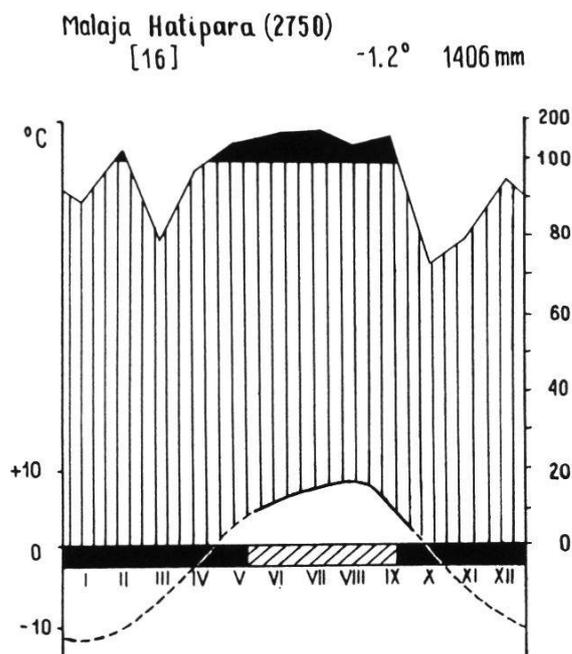


Fig. 1.2. Climatic diagram of meteorological station "Meadow - 5" on Mt. M. Hatipara.

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).

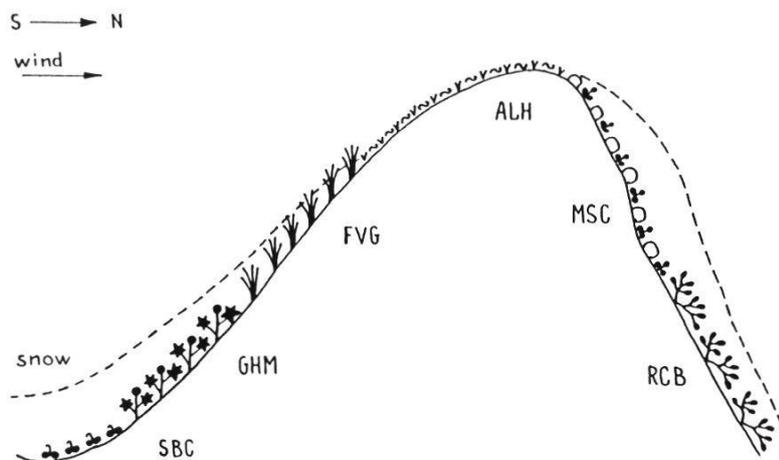


Fig. 1.3. Distribution of investigated communities over mesorelief forms. ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* meadows, SBC = snow bed communities, MSC = communities on moist screes, RCB = *Rhododendron caucasicum* 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 *Violo oreadis-Festucetum variae* and *Hedysaro caucasicae-Geranieta-um gymnocauli*, correspondingly. Abundance values according to the Braun-Blanquet scale.

* see Table 1.7.

Communities	FVG			GHM		
	U	L	K1	U	L	K1
Sample area						
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. adzhaticum* (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.