2. Site description and methods

2.1. Geography

Teberda State Reserve is located on the northern macroslope of the western Caucasus in the Karachaevo-Cherkessian Republic of Russia. The total Reserve area is about 850 square km. The main section of the Reserve occupies the upper reaches of the Teberda river valley between 41° 35' and 41° 55' E, 43° 13' and 43° 28' N (Fig. 1).

There is a considerable elevation range within the Reserve between the lowest (bottom of the valley, 1259 m a.s.l.) and the highest (Mt. Dombai-Ulgen, 4046 m a.s.l.) points. About 83% of the Reserve territory lies above 2000 m a.s.l.

The hydrological network is well developed. Overall, there are 130 glacial lakes and 30 rivers. All rivers belong to the Teberda river watershed. Lakes and rivers cover about 0.3% of the reserve area (POLIVANOVA 1990).

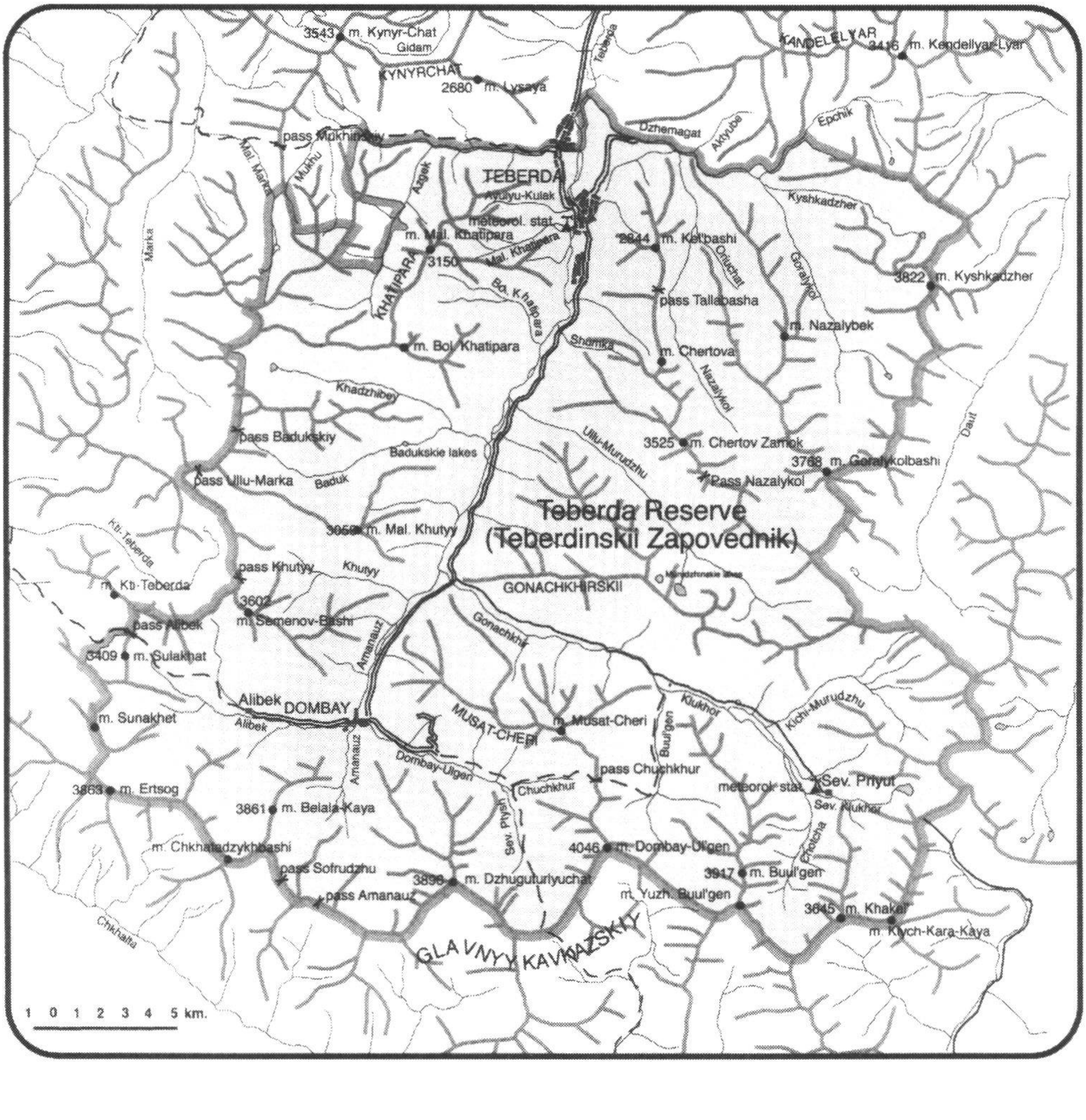
Three main geological factors have shaped the relief, namely glacial processes (ancient and modern), water erosion, slope processes, including avalanches, rock falls and creep processes. There are 85 existing glaciers, occupying about 10% of the reserve area.

The late Pleistocene glaciers covered most of the mountains from their summits to about 2400 m. The valley glacier extended down to 1300 m (elevation of the town of Teberda) and even lower (SHCHERBAKOVA 1973). The U-shaped ("trog") form of many valleys indicates their former glaciation. TUSHINSKIY (1957) described four phases of the local glaciation during the Holocene. Since 1850 the glaciers have been steadily retreating.

Outcrops (rocks and screes) are well represented in all vertical zones, but their role is most important in the alpine and subnival zones. They cover about 26% of the area of the Reserve.

Permafrost relief forms are restricted to several high stone ridges above 3400 m. The distribution of permafrost is, therefore, very limited and permafrost has negligible influence on the vegetation.

Fig. 1. A map of Teberda reserve

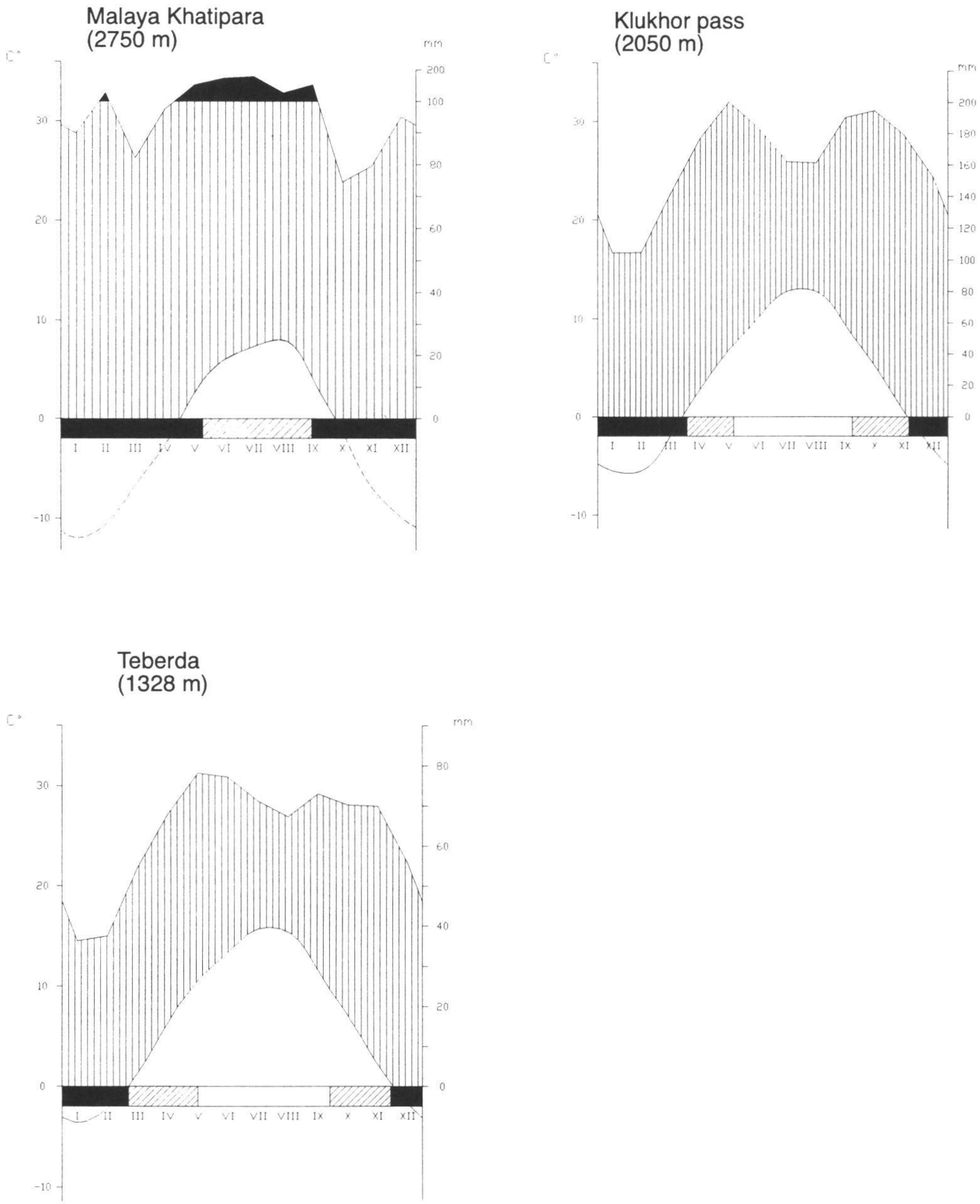


2.2. Climate

There are two permanent state meteorological stations in the Reserve, Teberda and Klukhor Pass (Fig. 1). Climatic diagrams of the stations are presented in Fig. 2.2-2.3. The climate of different parts of the Reserve varies considerably due to two main factors: elevation and distance from the Main Caucasian Range (south boundary of the Reserve). Overall, mean temperature decreases by 0.5-0.6 °C with 100 m increase in altitude. Precipitation increases with altitude up to about 2200-2500 m. Moist air masses are brought mainly by south winds from the Black Sea. Thus, precipitation sharply decreases from the Main Caucasian Range northward. South winds are predominant in the area, with the south slopes being windward and north slopes leeward with heavy snow accumulation (snow beds) determining the pattern of vegetation cover.

A typical climatic diagram for alpine zone in the northern part of the Reserve (Malaya Khatipara, temporarymeteorological station) is represented in Fig. 2.1. The climate of the alpine zone can be considered as the mountain climate of the temporal zone (type X (VI), according WALTER *et al*. 1975). Mean annual temperature is about –1,2 °C and mean annual precipitation – 1400 mm. These features resemble those of some areas in the Swiss Alps, for example Weissfluhjoch (2667 m a.s.l.) near Davos (ZINGG 1961). Air humidity averages about 79% during the summer months. Average duration of time with 100% air humidity is about 4 hours per day. Insolation at the soil level is about one half of the potential because of the clouds (see GRISHINA *et al*. 1986). The warmest month is August with mean temperature + 8.3 °C, but frost can occur throughout the summer.

Fig. 2. Climatic diagrams of three metereological stations in Teberda Reserve



2.3. Geology and soils

Siliceous rocks are prominent in the Teberda reserve. Local outcrops of limestone are known from two km outside the northern reserve boundary. The main bedrock type is grey granite. Different kinds of schists (biotit, chlorite, etc.), as well as gneisses, are well represented on several mountain ranges.

Alpine soils of the reserve were studied by several authors (ANTIPOV-KARATAEV *et al.* 1936, SEREBRYAKOV 1957, SHAL'NEV *et al.* 1977, VLADYCHENSKIY & GRISHINA 1987, GRISHINA *et al.* 1993, MAKAROV *et al.* 1997, ONIPCHENKO *et al.* 1998). The authors followed the Soviet system of soil taxonomy. Since this system is not now commonly used in the West, below we describe the soil categories according to the International FAO system.

As a whole, a shallow profile and great stone content characterize mountain soils. For example, in the lower horizons at a depth of 40-50 cm the percentage of stones may reach 80%.

The main type of forest soil of the Reserve is Cambisol, in particular Humic Cambisol. This soil profile has O, A, B, and C, horizons. The organic horizon (O) is 5-10 cm thick and is divided into OL, OF and OH sublayers. Such differentiation is clearly defined in dark coniferous forests on northern slopes, but it does not occur in pine forests on southern slopes. The texture of the mineral horizons is coarse sandy loam. The B horizon is only slightly enriched by clay. The upper border of the C horizon lies at a depth of 50-70 cm. Soils on northern slopes are usually darker due to a high humus content (up to 11% C). Soils on southern slopes contain less humus and are also characterized by a thinner profile.

Humic Cambisols of the Teberda Reserve are acidic to slightly acidic (pH 5.5-6.5). An A-horizon with pH about 5.5 is considered as umbric, otherwise (pH > 6.0) it is mollic. The sum of exchangeable base cations is about 300-400 mmol/kg. Ca is the main exchangeable base cation.

The main subalpine and alpine grassland soils are Leptosols, most frequently Umbric Leptosols. Their soil profile consists of A, B, and C horizons. The A-horizon can be divided into two sublayers. The upper 10-cm sublayer is strongly penetrated by the roots of grasses, which constitute 4-11% of horizon volume. The lower sublayer above 20 cm does not form the firm turf. The texture of Leptosols is coarse sandy loam, clay is not differentiated throughout the profile. The upper border of the C horizon lies at a depth of about 50 cm. Morphological features of Umbric Leptosols in the alpine zone are similar to those of the subalpine zone. The only difference is that the alpine soils are shallower.

Properties of A horizons (0-10 cm) of subalpine and alpine Umbric Leptosols which are formed under different plant communities are shown in Table 2.1. The humus content of an acidic unsaturated Umbric Leptosol might be up to 20%. Soils also accumulate high amounts of total N and P. The humus contains a large proportion of slightly humified plant debris. This is primarily due to low microbial activity within the accumulated raw humus. The subalpine and alpine soils are poor in available nitrogen and phosphorus, but they are enriched by potassium due to potassium-rich parent rock material.

Umbric Leptosols of subalpine grasslands have pH 4.7-5.6 and total exchangeable base cations are about 150-170 mmol/kg. Soils of subalpine tall herbaceous communities, which are formed at the gently sloping positions disturbed by landslips and temporary streams, differ from soils of subalpine meadows. They accumulate less organic C and N and are characterized by relatively low concentrations of available $N(NH_4)$, while accumulation of total and available P is more expressed.

Alpine Leptosols are more acidic (pH 4.3-5.2), have lower base saturation (14-52%) and lower sum of exchangeable base cations (30-150 mmol/kg). We studied the change in the alpine soil properties along a catena at Mt. Malaya Khatipara (GRISHINA *et al.* 1993). It has been shown that the stone content decreases, while percentage of fine grained soil fraction, actual and hydrolytic soil acidity, content of exchangeable ammonium and storage of organic matter increases from the upper parts of slopes down to the snow bed depressions.

The study of alpine Leptosols under various plant communities, which occupy different positions along alpine toposequences throughout the Teberda reserve, confirmed some of our earlier findings. Alpine heath soils of ridges and prominent top part of slopes have the highest value of exchangeable base cations and relatively low concentrations of available N and P (Table 2.1.). The C:P ratio in these soils is large that testifies about impoverishment of organic matter by P.

The Leptosols of alpine meadows in typical slope positions are characterized by some decreasing of exchangeable base cations and increasing of available N and P relative to other alpine communities. Low concentrations of organic C may be caused by more active organic matter mineralization in the most favourable conditions of the alpine zone. Soils of slope depressions (ass. *Hedysaro caucasicae - Geranietum gymnocauli*) are more acidic and unsaturated with base cations.

Table 2.1.
Some properties of A horizons of investigated soils.
First column for all properties – mean value, second column – standard deviation, BS – rate of base saturation

Community	n	Depth, cm		N		P		$N(NH_4)_{av}$		$P_{avail.}$		pH (H2O)		Hydrolytic acidity		K		Ca		Mg		BS	
								mg/kg						mmol/kg								%	
Hyalopoo ponticae-Pedicularietum nordmannianae	15	10	3	0,75	0,17	0,15	0,03	43	13	19	13	4,3	0,2	233	68	8	4	25	17	6	2	14	7
Caro caucasici-Caricetum nigrae	13	16	9	0,99	0,61	0,12	0,04	34	25	57	40	5,4	0,4	96	65	7	6	92	89	17	17	52	21
Ranunculetum brachylobi	13	8	3	0,43	0,16	0,11	0,02	32	19	39	38	4,6	0,2	131	58	4	1	20	3	5	1	21	8
Hedysaro caucasicae-Geranietum gymnocauli	15	10	4	0,70	0,12	0,11	0,02	46	10	17	8	5,0	0,3	181	39	7	2	46	20	9	5	26	10
Pediculari comosae-Eritrichietum caucasici	15	12	5	0,85	0,21	0,13	0,04	28	14	6	4	4,8	0,3	128	36	7	3	85	57	16	11	43	18
Polygono viviparum-Salicetum kazbekensis	14	11	4	0,95	0,19	0,10	0,03	31	16	10	6	4,9	0,2	178	40	5	1	87	62	17	8	38	7
Violo altaicae-Festucetum variae	13	18	8	0,84	0,19	0,12	0,04	35	11	28	18	4,7	0,3	119	51	7	3	70	35	14	8	44	16
Rhytidio rugosi-Kobresietum capilliformis	13	11	1	0,88	0,27	0,14	0,07	25	10	13	5	5,2	0,2	138	25	7	2	118	35	23	7	52	7
Cephalario giganteae-Ligusticetum alani	13	23	13	0,70	0,25	0,13	0,03	34	16	56	46	5,6	0,3	99	39	1	6	134	52	27	13	63	10
Anthrisco sylvestris-Rumicetum alpini	11	14	6	0,70	0,31	0,18	0,05	31	15	69	56	4,7	0,4	109	28	8	4	112	65	29	21	54	13
Lerchenfeldio-Rhododenretum caucasici	11	19	7	1,12	0,32	0,10	0,02	24	19	35	12	3,8	0,5	161	111	1	4	157	69	38	18	58	23
Aconito nasuti-Juniperetum	14	16	6	1,14	0,27	0,13	0,03	33	18	14	5	4,5	0,4	130	92	7	2	144	39	24	6	62	20
Betonici macranthae-Calamagrostietum arundinaceae	17	15	4	0,98	0,14	0,10	0,02	45	13	16	11	5,1	0,3	133	30	9	3	121	36	27	9	54	9
Swertio ibericae-Caricetum nigrae	12	28	12	1,76	0,55	0,11	0,04	45	22	48	32	5,7	0,3	43	10	22	13	287	102	53	21	89	5

The most acidic and unsaturated soils are formed at the low end of the alpine hydrologic gradients (soils of alpine snowbeds). However soils of these two communities are differed from one to another. Development of *Ranunculetum brachylobi* in accumulative positions near the upper boundary of the alpine zone causes relatively low concentrations of soil C, N and P, while in soils of *Hyalopoo ponticae-Pedicularietum nordmannianae* accumulation of organic matter and associated elements is more expressed.

Among alpine soils the Leptosols of *Kobresia*-grasslands are characterized by the highest value of pH, exchangeable cations and base saturation, as these soils are formed in areas of distribution of easily-weathered porphyritic granite. It seems to us that the comparatively high ammonium content in the soils of alpine grassland is caused by disturbance regime (TILMAN 1988), while the same in the soils of snow bed communities is connected with the short vegetative season that prevents full uptake of ammonium by plants.

Histosols are another type of subalpine and alpine soil. Terric and Fibric Histosols are formed in swamp communities and Folic Histosols are the soil of *Rhododendron caucasicum* elfins. All Histosols are characterized by the high level of C and N accumulation and have high C:N and C:P ratios. Nevertheless the Histosols of dry and moist positions differ strongly in acidity and available nutrients concentrations. Histosols of subalpine and alpine swamps contrary to Leptosols have high value of pH, total exchangeable base cations and base saturation, while their hydrolytic acidity is the lowest. Moist Histosols contain also high concentrations of available N and P. Folic Histosols contrary to swamp soils have low pH and available N and P concentrations. Hydrolytic acidity of these soils is very high, which determines the low base saturation in spite of high amount of base cations.

There are no signs of podzolization in the alpine soils. Only a low rate of gleization can be observed in the soils of snow beds with water saturation during the rather short snow-melting period. Thus, alpine soils of the area differ considerably from podzolic and pseudoglei soils of the Alps (BOUMA *et al.* 1969; BOUMA & VAN DER PLAS 1971; GRACANIN 1972; POSCH 1977; NESTROY 1984; MULLER 1987), but they are similar to the Alpine Turf soils of the Rocky mountains (Colorado) (RETZER 1956, 1974; JOHNSON & CLINE 1965) and to the Alpine Humus Soils in Australia (COSTIN *et al.* 1952; COSTIN 1955).

2.4. Flora and vegetation zones

As in any mountain flora, the flora of Teberda reserve is rather rich. VOROB'EVA & KONONOV (1991) list 1280 vascular plant species for the reserve. The flora of bryophytes contains 73 liverworts and 227 leafy mosses (IGNATOVA *et al.*, 1990). Recently we added to the lists 30 vascular plants species and 67 mosses (ONIPCHENKO & IGNATOVA 1996). Similar floristic richness is known for other mountain regions in Europe, for example, Davos (SCHIBLER 1937).

The main life form groups of vascular plants are herbaceous polycarpic perennials (75%), annuals (11%), trees and shrubs (8%) and monocarpic perennials (4%) (VOROB'EVA & KONONOV 1991). There are 23 threatened species listed in the "Red Data Book of Russia" in the reserve.

Four main vegetation zones are well represented in the reserve, namely forest, subalpine, alpine and subnival zones. The total number of plant species decreases from the forest through subalpine and alpine to the subnival zone: 900, 373, 206, and 122 species respectively (VOROB'EVA & KONONOV 1991).

Forests cover about 34% of reserve area. Five species of trees are the most common (occupied part of the total forest area is represented in parenthesis, %): Scots Pine (*Pinus sylvestris*) (34.7), Litwinov's birch (*Betula litwinowii*) (27.1), Caucasian Fir (*Abies nordmanniana* (12.6)), Caucasian spruce (*Picea orientalis* (8.4)), and Caucasian beech (*Fagus orientalis* (3.3)) (VOROB'EVA *et al.* 1986).

Pine forests are more typical of the northern part of the reserve. They occupy mainly southern and eastern dry slopes from the valley bottom up to the timberline. Climatic upper timberline of the area lies at 2500-2600 m, but the actual timberline lies at lower altitude (2200-2350 m). Dark coniferous forests are well developed in the moist southern part of the reserve near the Main Caucasian Range. They prefer valley bottoms on northern and western slopes. Birch forests replace conifers near the timberline (2000-2200 m) and across avalanche paths. Short birch forests (5-12 m) and *Rhododendron caucasicum*-elfin woods (subalpine shrub community) are typical of northern slopes near the timberline. Dwarf pine and alder elfin woods, common in the Alps, are notably absent in the vegetation of the Caucasus.

Traditionally the area above the timberline is considered as the alpine zone (sensu lato) in temperate mountains (ELLENBERG 1988, WALTER & BRECKLE 1986). Most Caucasian botanists, however, (GROSSGEIM 1948, SHIFFERS 1953, KONONOV 1957, VOSKANYAN 1977 et al.) do not hold this point of view. Traditionally, they divided the area into three zones: subalpine, alpine (*sensu stricta*) and subnival. The subalpine zone lies near and above the actual timberline up to the climatic timberline. We can easily distinguish this zone from the alpine zone by the type of plant communities developing in snowed depressions. Communities of *Mulgedio-Aconitetea* are typical for such places in the subalpine zone. In the alpine zone (*sensu stricta*) communities belonging to another class - *Salicetea herbaceae* - occupy snowbed depressions. The more favourable temperature regime in the subalpine zone leads to intensive spring snowmelt, which prolongs the vegetative season in snowbeds as compared with the alpine zone.

The snow line in the region is located at about 3000 m. This elevation can be considered as a border dividing the alpine and subnival zones. Sparse plant communities on rocks and screes alternating with glaciers and snowfields are commonly found in the subnival zone. According to our observations, the upper limit of vascular plant distribution here is approximately 3750 m. Several species (*Saxifraga moschata, S.sibirica, Draba rigida, D.siliquosa, Minuartia imbricata, Primula meyeri, Senecio karjaginii, Potentilla gelida, Carum caucasicum, Hyalopoa pontica*) reach this elevation on the southern slope of Mt. Kyshkadzhar.

2.5. Animals

The fauna of the reserve is also rich, but only a few systematic groups have been investigated in detail. Birds and mammals play an important role in alpine ecosystems. There are 22 nesting bird species in the alpine zone (POLIVANOVA 1990). The grouse family [*Tetraogallus caucasicus* (Pallas), *Alectoris kakelik* (Falk), *Lyrurus mlokosiewiczi* Taczanowski] are prominent plant consumers and seed dispersers, especially of berry-producing plants (*Juniperus communis, Empetrum nigrum, Vaccinium spp.*, etc.).

Wild ungulates are represented in the alpine zone by three species: Caucasian ibex (*Capra caucasica* Guldenstaedt et Pallas), chamois (*Rupicarpa rupicarpa* L.) and wild boar (*Sus scrofa* L.) (SOKOLOV & TEMBOTOV 1993). Population density of these species is mainly restricted by the availability of winter food and illegal hunting. The intensive grazing of ibexes takes place on protected areas free from snow (rock outcrops, *Anemonion speciosae* - alpine heaths).

A vole *Pitymys majori* Thos. is the most abundant rodent in the alpine zone. This polyphagous vole includes the a large number of alpine plant species in its diet. Population density of this animal varies considerably among different plant communities (FOMIN *et al.* 1989). Moreover, the intensive burrowing activity of *Pitymys majori* as well as large mammals like wild boars and bears (*Ursus arctos* L.) plays an important role in disturbing the alpine grasslands (ONIPCHENKO & RABOTNOVA 1994).

2.6. History of human influence

The first evidence of human activity in the Teberda valley dates from the Bronze Age (Koban culture, XII-X century B.C., ALEKSEEVA 1992). There are numerous archaeological sites of early Middle Age settlements in the reserve area. It is safe to assume that the human influence on the vegetation in the area has lasted for at least two millennia. Alpine areas have been greatly transformed by cattle and sheep grazing. Cattle number was never too high due to the restricted area of winter pastures until XX century. Moreover, the rate of grazing has fluctuated considerably. Periods of brutal wars and devastating plague epidemics with consequently negligible grazing alternated with periods of peace, when number of cattle increased (TSEPKOVA 1986, DINESMAN 1992). The last plague epidemic in the Teberda region took place at the beginning of the XIX century.

Intense use of the area resumed at the end of the last century due to building of the War-Sukhumian Highway across the Klukhor pass. The town of Teberda was founded at this time as a summer cottage village.

Teberda Reserve was founded in 1936. Cattle grazing in the alpine area of the reserve continued, however, until 1943. Many of the alpine communities show signs of former grazing in their structure and composition.

Recent economic difficulties exert an adverse effect on nature protection in the region. The administration of the reserve has had to permit grazing in several areas within its boundaries (Kyshkadzhar, Goralykol, and bottom of Teberda valley), leading to further transformation of the vegetation in such areas.

2.7. Methods

We collected releves of different vegetation types during 1980-95. The total number of releves is about 700. The studied area covers the Teberda reserve and adjacent neighbouring valleys and crests (Mukhu, Gidam, Epchik, Kyr-kol, etc.). The size of releve area ranged between 9 and 100 square m depending on the type of community. For herbaceous vegetation MIRKIN & ROZENBERG (1978) recommended using plots which contain about 80% of species from 100 sq.m- plots. We tried to follow this rule. Our study of floristic richness of the alpine communities (ONIPCHENKO & SEMENOVA 1988, 1995) showed that such plot size lies mainly within 10-25 sq.m. As a rule, larger plots were used for sparse vegetation (rocks, pebbles, screes etc). The Braun-Blanquet scale was used as a value of species abundance.

Samples of bryophytes and epigeal lichens were collected from releve plot. All bryophytes were determined by E.A.Ignatova.

The Nomenclature of the Caucasian plants is not well developed. Most regional floras (GROSSGEIM 1949; KOSENKO 1970; GALUSHKO 1978-80; VOROB'EVA & KONONOV 1991), as well as the general vascular plant checklist for Russia (CZEREPANOV 1995), use the "micro-species" (splitting) approach. We had to study nomenclature of each species separately in different publications, including a current review of some groups and floras of neighbouring countries (DAVIS 1965-1980). Full names and main synonyms of vascular plants are represented in the species index.

We use WIRTH (1980) as a main source of lichen names. Bryophyte nomenclature is based on checklists for the former Soviet Union (IGNATOV & AFONINA 1992, KONSTANTINOVA *et al.* 1992).

Special IBM-program "Syntaxon" (OVCHINNIKOV & ONIPCHENKO 1992) was created for data processing according to the classical table method of Braun-Blanquet. The program allows a numerical approach to be combined with hand procedures in a colour visual regime. MVSP software was used for Cluster and Detrended Correspondence Analysis (KOVACH 1995).

The general category of diagnostic species (characteristic and differential species together) was used in our work. Several monographs and syntaxonomic reviews (OBERDORFER 1977, 1978, 1983, 1992, MATUSZKIEWICZ 1981, MORAVEC *et al.* 1983, MIRKIN *et al.* 1989, JULVE 1993, MUCINA *et al.*, 1993) served as a source of information on the diagnostic species combinations for the European syntaxa.