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TECHNIQUES AND STRATEGIES

The structure and dynamics of alpine plant communities in the Teberda Reserve, the Northwestern Caucasus

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Abstract. Results of long-term ecological investigations in four different alpine communities are discussed. The structure differs considerably between communities within the alpine zone. Meadows and grasslands with moderate snow depth have the highest vascular plant biomass and annual production. Plant productivity decreases in snow free communities (alpine lichen heaths) as well as in snow bed communities.

Populations of most of the alpine species consist of groups of all ontogenetic stages. Soil seed banks in meadows and snow bed communities are greater than in grasslands and lichen heaths. Most of the alpine species (77%) have mycorrhiza. Vesicular-arbuscular mycorrhiza is most common.

Seasonal dynamics, year-to-year fluctuations and long-term successions are discussed.

Alpine lichen heaths have a specific spatial structure: lichen patches alternate with patches 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 larger area than their above-ground shoots do. Thus, some vacant space becomes available for fruticose lichens as there is no significant competition for nutrients with vascular plants. Several experiments (removal of lichens, fertilization, root cutting) was carried out to prove the hypothesis.

Most of the alpine species were sensitive to the light deficit. Evergreen species were relatively tolerant of an artificial shading.

Keywords: lichen heaths, snow bed communities, phytomass, seed banks, competition, experiments

Introduction

The problem of species coexistence is one of the most fundamental ones of modern ecology. Up to present, about twenty of mechanisms controlling species-richness maintenance in plant communities were discussed (Grubb 1977; Shmida and Ellner 1984; Braakhekke 1985; Denslow 1985; Tilman 1988, 1990; Smith and Huston 1989; Wilson 1990; Zobel 1992). Consequently, there is a need to study many of different features of a community in order to understand the relative role of the different mechanisms. Clearly it is necessary to have a detailed description of the community and its components first.

Due to the relatively small human impact, alpine communities may serve as particularly suitable objects for ecological research. Since 1979 the group of researches from Moscow State University has been investigating the alpine communities of the Northwestern Caucasus, attempting to analyze their structure and dynamics. The aim of this paper is to review the main results of the research achieved within a 10 year period (1979 - 1989). Most of the results were published only in Russian (Onipchenko 1984, 1985, 1990; Semenova and Onipchenko 1989, 1990, 1991; Onipchenko et al. 1991, 1992 etc.).

Study area and description of communities

The study area is located in the alpine zone of the Mount Malaya Hatipara, Teberda Reserve, Karachai, the NW Caucasus, Russia 43° 16' N, 41° 41' E; altitude: 2,700 - 2,800 m.

A catena (toposequence) of alpine communities with different snow-depth was studied. Four plant communities were investigated, such as Alpine Lichen Heath (ALH), *Festuca varia*-Grassland (FVG), *Geranium gymnocaulon - Hedysarum caucasicum* Meadows (GHM) and Alpine Snow Bed communities (SBC). Brief characteristics of the examined plots are represented in Table 1. Syntaxonomy follows Onipchenko, Minaeva and Rabotnova (1987), Onipchenko *et al.* (1992), the data on floristic richness are compiled from Onipchenko and Semenova (1988). See Appendix 1 for vascular plant nomenclature.

(1) The alpine lichen heath is dominated by fruticose lichens (mostly *Cetraria islandica*). This type, belonging to the Pediculari chroorrhynchae-Eritrichietum caucasici Minaeva 1987 (Juncetea trifidi), occupies windward crests and slopes. The mean floristic richness is 14.8 and 36.0 vascular plant species per plots of 25 x 25 cm and 5 x 5 m, respectively. *Festuca ovina, Carex sempervirens, C. umbrosa, Campanula biebersteiniana, Anemone speciosa* and *Antennaria dioica* are the dominant vascular plant species forming more than 5% of the aboveground biomass.

(2) The *Festuca varia* grassland (Violo oreadis-Festucetum variae Rabotnova 1987) is a firm-bunch grassland with great accumulation of dead plant material in the aboveground layer. These grasslands are floristically rich (11.1 and 48.6 species per plots of

Community type	ALH	FVG	GHM	SBC
Relief forms	crests,ridges, windward slopes	slopes (often steep)	leeward slopes & small depressions	bottoms of deep depressions
Depth of snow cover in winter (m)	0-0.3	0.5-1.5	2 - 4	5 and more
End of snow melting	April/May	end of May /first half of June	June/first half of July	July/ first half of August
Duration of vegetation period (months)	4.5-5.5	3.5-4.5	2.5-3.5	1.5-2.5
Aspect	S	SSW	SW	SW
Slope (°)	15	10	5	1
Number of the vole burrows per hectare (average ± s.e.,n=25)*	300±110	1500±290	3700±590	30±30

Table 1. General characteristics of the studied communities. Legend: ALH: Alpine Lichen Heath; FVG: *Festuca varia* Grasslands; GHM: *Geranium gymnocaulon-Hedysarum caucasicum* Meadows; SBC: Alpine Snow Beds.*/ following Fomin, Onipchenko and Sennov (1989)

25 x 25 cm and 5 x 5 m, resp.). *Festuca varia* and *Nardus stricta* are dominants.

(3) The forb-rich meadows *with Geranium gymnocaulon* and *Hedysarum caucasicum* (Hedysaro caucasicae-Geranietum gymnocauli Rabotnova 1987) develop on sites with a high snow cover and short vegetation period (about 3 months). *Geranium gymnocaulon, Hedysarum caucasicum, Festuca brunnescens, Deschampsia flexuosa, Nardus stricta, Phleum alpinum* and *Anthoxanthum odoratum* are the dominant species. The floristic richness is 11.4 and 30.6 species per plots of 25 x 25 cm and 5 x 5 m, resp.

(4) The alpine carpet-like snow-bed communities of the Hyalopoo ponticae-Pedicularietum nordmannianae Rabotnova 1987, Salicetea herbaceae, occupy depressions. Short rosette and draft -trailing plants, such as *Sibbaldia procumbens, Taraxacum stevenii, Gnaphalium supinum, Minuartia aisoides,* and tussocky *Nardus stricta* are the dominants. The floristic richness is 7.9 and 18.0 species per plots of 25 x 25 cm and 5 x 5 m, resp. Probably the lowest species richness in the SBC might be connected to severe abiotic stress (thick snow cover and short vegetation period).

The soils of all communities have developed on siliceous rock (biotite schists and granites). The soils are classified as Alpine Meadow-mountain Soils (Egorov *et al.* 1977) or as Cryorthents of USDA Soil Classification (Soil Survey Staff 1967). There are no signs of podzolization or gleization, which would distinguish our soils from the widespread high-mountain soils of the Alps (Bouma *et al.* 1969; Bouma and van der Plas 1971; Müller 1987). Some characteristics of the soils are represented in Table 2. A more detailed description of the soils is given in Grishina et al. (1993). The burrowing activity of pine voles *(Pitymys majori* Thos.) has a great impact on soils and plants in the GHM, and increases water permeability of soils in this community (Table 2).

The different groups of heterotrophs (animals and fungi) were investigated in the alpine communities. The results of these investigations are summarized in Onipchenko and Jakova (1994) for large soil invertebrates, Polivanova and Shevchenko (1987) for birds, Fomin, Onipchenko and Sennov (1989) for small mammals, Leinsoo *et al.* (1991) for soil fungi, and Onipchenko and Kaverina (1989) for mushrooms.

Cryptogamic components of the communities

Soil-dwelling and epiphytic algae

64 species of soil-dwelling and epiphytic free-living algae were found in the ALH (19 species of *Cyanophyta*, 31 - *Chlorophyta*, 8 - *Bacillariophyta*, and 6 - *Xanthophyta)*. The biomass of algae attained 1.2-1.6 g of fresh weight/m^2) (Leinsoo, Onipchenko and Shtina 1987). Fewer algae species were found in the GHM and the SBC (Shtina, personal communication).

Lichens

Epigeous lichens are most abundant in the ALH. There are more than 12 fruticose lichens species in

Community	ALH	FVG	GHM	SBC
Depth of humus layers (cm)	15-20	20-24	19-22	16-17
pH (water) of upper layer	5.6	5.1	5.1	4.7
pH (KCl) of upper layer	4.0	4.0	4.1	3.8
content of soil skeleton in 0-10 cm (volume %)	13	10	9	5
organic substance (ignition loss) in 0-10 cm (%)	18	23	22	29
total N in the upper layer (%)	0.77	0.73	0.56	1.32
humus store in the 0-40 cm (kg/m²)	15.6	19.6	23.0	32.5
water filtration coefficient (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

Table 2. Selected soil properties of the alpine communities (from Onipchenko, Vanjasin and Selesneva 1985; Grishina et al., 1993).

the ALH, *Cetraria islandica* is dominating by its biomass of 230-430 g of dry weight/m²) (Onipchenko 1982). The role of lichens in other communities is negligible (Table 3).

Bryophytes

There are more than 300 bryophytes species in Teberda Reserve (Ignatova, Váňa and Vorob'eva 1990). Still only a few of them were found in the investigated communities, and their biomass was low (less than 10 g/m²). The most common were *Polytrichum piliferum* Hedw. and *P. juniperinum* Hedw. These species were found in all studied communities.

Mycorrhiza of alpine plants

120 alpine vascular plant species were investigated for mycorrhiza. Vesicular-arbuscular mycorrhiza was found in 83 plant species, ericoid mycorrhiza - in 4 dwarf shrubs, orchid mycorrhiza in 3 Orchids, and ectomycorrhiza in 2 species, such as *Salix kazbekensis, Polygonum viviparum* (Baikalova and Onipchenko 1988).

28 species (23% of all studied species) had no mycorrhizal infection. As a rule, the most abundant species had a greater rate of infection than others. The level of mycorrhizal infection was high in spring, decreasing during the flowering period, and increasing again by in autumn.

Mycorrhizal fungi infect host plants at the first stages of development from seeds. Seedlings and juvenile individuals of alpine species usually have a greater level of infection than the adults (Baikalova and Onipchenko 1988).

Phytomass and production

The composition of above- and belowground phytomass was investigated for alpine communities; the aboveground biomass was determined for the main species (Onipchenko 1985, 1990). The FVG and the GHM had the highest vascular plant biomass (on average 306 and 318 g/m² resp.; Tab. 3). Lichen biomass exceeded 400 g/m² in ALH (Onipchenko 1982).

The aboveground necromass was the highest in FVG (about 900 g/m²). This is due to a high production of the community, and to a low rate of decomposition of dead leaves of firm-bunch grasses (Leinsoo *et al.* 1991). The belowground phytomass (biomass + necromass) was the highest in GHM (about 1,900 g/m²). The belowground biomass was three times as much as necromass in this community. In the other investigated communities belowground biomass only slightly exceeded the necromass.

We estimated the total annual netto-production for the investigated communities to be 150, 400, 550 and 200 g/m² for ALH, FVG, GHM, and AK, resp. So a moderate winter snow depth in the GHM is relatively favorable for plant production in the alpine zone. Plant

Community	ALH	FVG	GHM	SBC
Aboveground phytomass (n=60):				
vascular plants	113± 7	306±17	318± 20	129± 5
lichens	440±23	36±2	6±3	2±1
mosses	3± 3	9±2	2± 2	3±1
litter+necromass	229±17	909±104	200±17	156± 28
Belowground phytomass (n=10):				
biomass	478±42	636±34	1392±177	944±128
necromass	403±38	565±46	4910±49	592±38

Table 3. Phytomass of the alpine communities (g/m², average and standard error, dry mass) (from Onipchenko 1985, 1990). For abbreviations of the communities see Tab.1

Species	ALH	FVG	GHM	SBC
Anthoxanthum odoratum	0	20±9	155±61	5±5
Carex atrata	0	170±42	75±20	45±21
Carex oreophila	0	0	0	35±13
Carex umbrosa	25±5	5±5	10±7	0
Cerastium purpurascens	0	100±61	0	0
Euphrasia ossica	0	100±63	10±10	0
Festuca ovina	15±15	75±55	20±9	10±7
Festuca varia	0	5±5	5±5	0
Gentiana djimilensis	40±20	10±10	0	0
Geranium gymnocaulon	0	0	0	0
Gnaphalium supinum	0	0	0	1475±333
Hedysarum caucasicum	0	0	0	0
Luzula multiflora	0	20±16	1600±406	90±61
Matricaria caucasica	0	0	1190±196	25±12
Nardus stricta	0	455±190	210±58	20±12
Phleum alpinum	0	0	175±82	10±7
Sibbaldia procumbens	0	0	110±38	765±187
Taraxacum stevenii	0	0	0	245±115
Veronica gentianoides	45±45	25±12	150±71	5±5
Sum (seeds)	350±160	1190±194	3850±481	2810±422
Gagea glacialis (bulbs)	0	510±193	2840±629	990±358

Table 4. The composition of the soil seed banks in the studied communities (number of seeds per m², average± standard error, n=20). Only the most common species are listed (from Semenova and Onipchenko 1990).

productivity decreased in snow free communities with deep soil freezing as well as in snow-bed communities with a short growing season (Onipchenko 1990).

Specific features of the biological turnover were investigated for ALH (Voronina, Onipchenko and Ignat'eva 1986). Si, Ca, N, and P are the prevailing mineral elements occurring in the phytomass. The turnover is slow, and the period of litter -fall decomposition exceeds 20 years. Thus the biological turnover has properties similar to those of the alpine tundra ecosystems and grasslands (Ignatenko and Berman 1979; Titljanova 1979; Basilevich 1984; Voronina, Onipchenko and Ignat'eva 1986).

Population biology of alpine plants

Composition of populations

Populations of most of the alpine species consist of all groups of developmental stages (from seedlings to mature plants) (Semenova and Onipchenko 1989). The following species have the normal type of population structure (sensu Rabotnov 1950): *Anemone speciosa, Campanula biebersteiniana, Festuca varia, F.brunnescens* and *Geranium gynmocaulon*. Until 1943 the study area had been used as a pasture. Effects of grazing in the composition of populations can still be recognized. Old and mature plants with morphological signs of senescence are predominant in the populations of grazing-tolerant species *(Nardus stricta, Sibbaldia procumbens, Gnaphalium supinum)*, while the juvenile and young individuals are numerous in populations of grazing-intolerant species (e.g. *Carum caucasicum, Campanula biebersteiniana, Hedysarum caucasicum)* (Semenova and Onipchenko 1989).

Soil seed banks

The banks of viable diaspores in the soil were studied using two germination methods: (1) germination from soil samples for 3 years in the greenhouse, and (2) counting of seedlings in situ after artificial soil disturbance (Semenova and Onipchenko 1990, 1991). The number of seedlings recorded with the Method 1 was significantly higher than that with the Method 2.

The number of viable seeds per m² (Method 1) averaged 150-510 in ALH, 1,000-1,380 in FVG, 2470-5,230 in GHM, and 1,590-4,030 in SBC (Table 4). The correspondence between recent plant composition and soil seed-banks was obvious in the ALH, where

Community	species richness	
	community	seed bank
FVG	4.6±0.6	3.7± 0.4
GHM	5.3±0.5	5.4± 0.4
SBC	5.1± 0.3	4.2± 0.4

Table 5. Floristic richness of the alpine plant communities and their soil seed banks (number of species per 100 cm², average and standard error, n = 20, depth of soil samples 0-10 cm; from Semenova and Onipchenko, 1990)

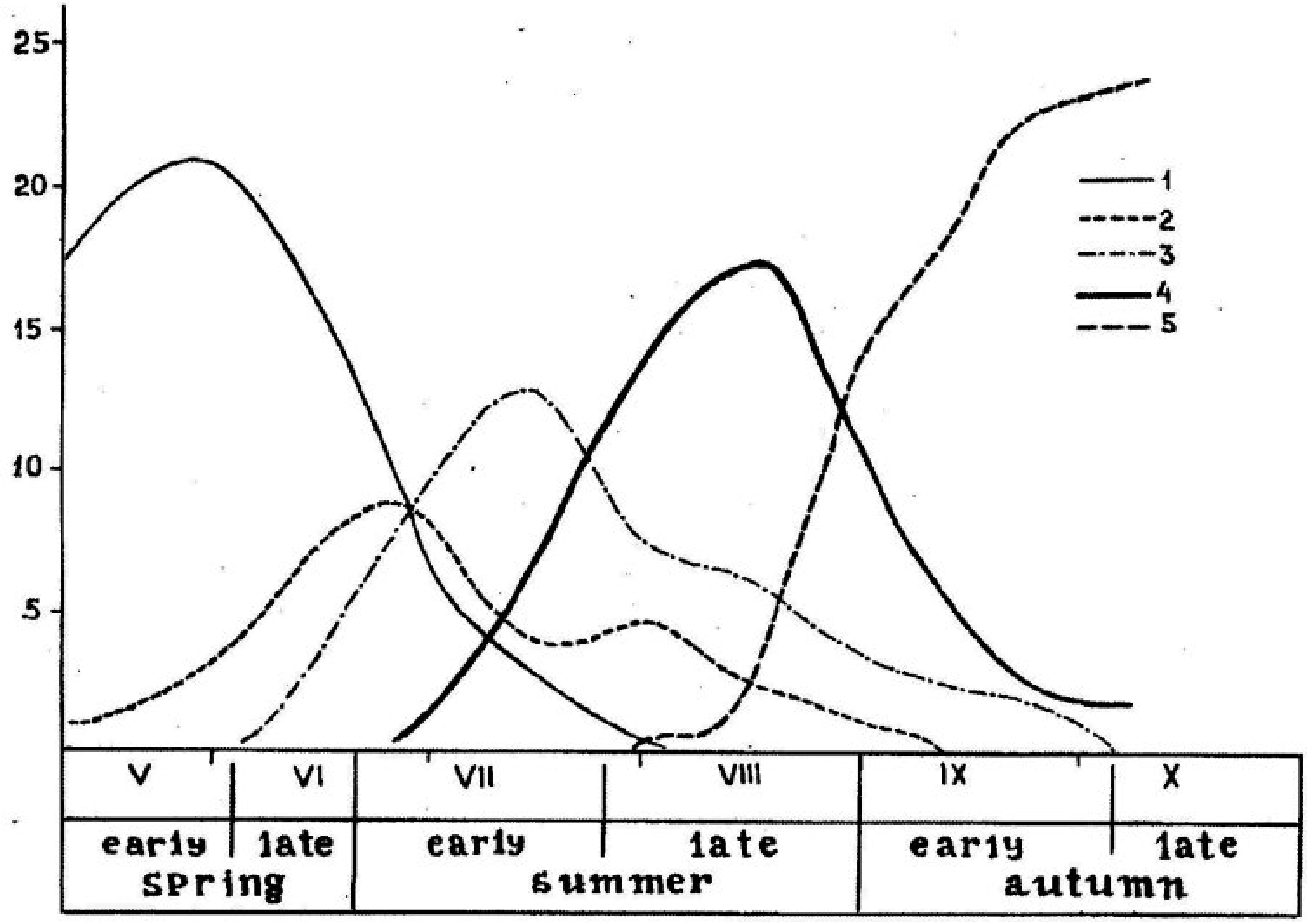

Fig. 1. Phenological curves for the Alpine Lichen Heath. Ordinate: the number of species in a particular phenological phase; abscissa: time and phenological period. Phenological phases: 1 - vegetative, 2 - budding, 3 - flowering, 4 - maturation of fruits, 5 - dissemination (from Onipchenko 1983).

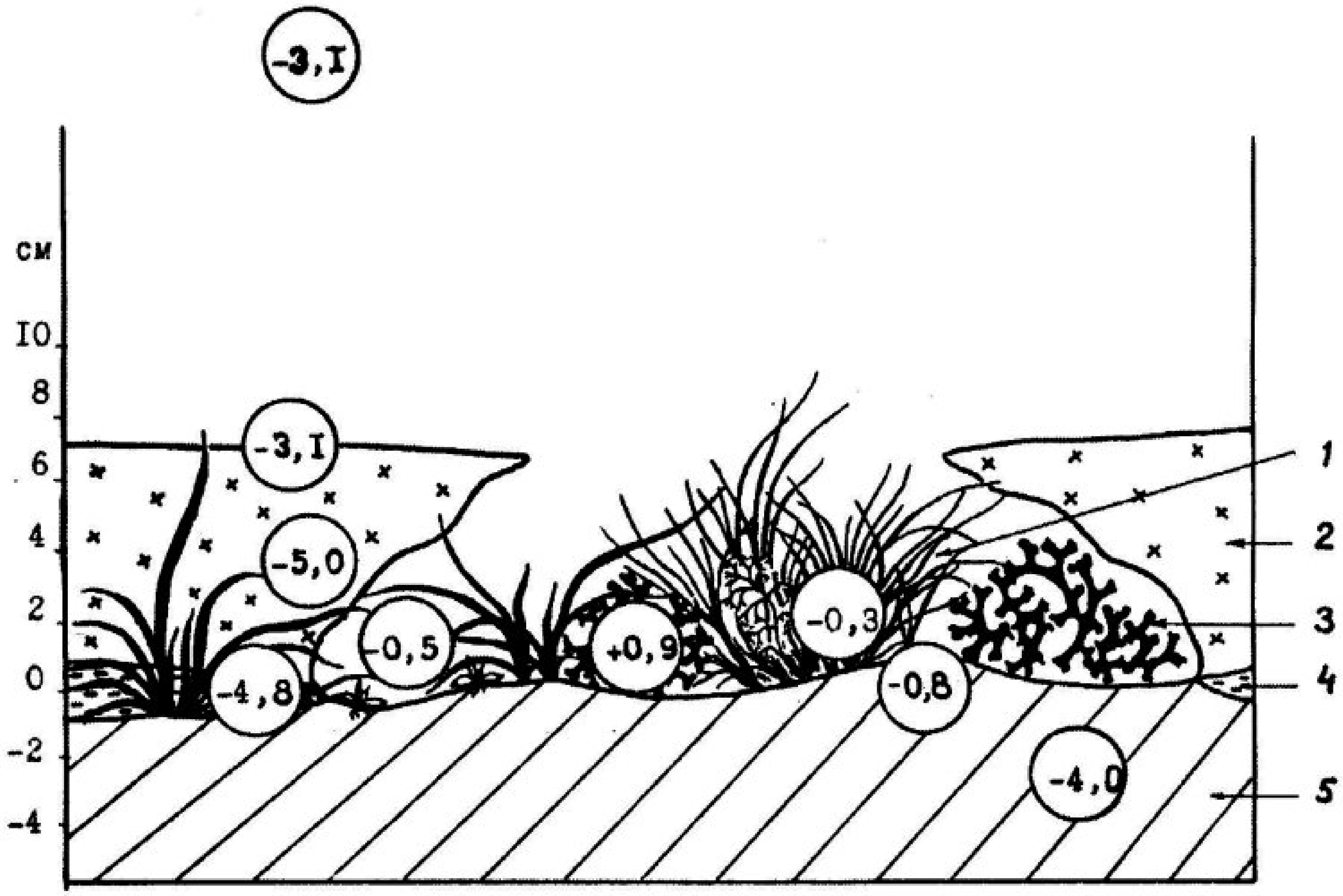

Fig. 2. The temperature pattern at a winter thawed patch (measured at noon January 25, 1981): 1 - *Festuca ovina* sod, 2 - snow, 3 - *Cetraria islandica* mat, 4 - ice crust on the soil surface, 5 - the upper soil layer (from Onipchenko 1983).

a positive correlation (r =0.60, n= 18, p<0.01) between the number of viable seeds in soil and annual seed production was found. On the contrary, the viable seeds of the most abundant species of the FVG *(Festuca varia)* and the GHM *(Geranium gymnocaulon, Hedysarum caucasicum)* were nearly absent from soils.

Seeds weighing more than 4 mg do not occur in the alpine soil banks. The most abundant species in the seed banks (more than 100 seeds/m^2) have small seeds weighing less than 0.7 mg. The floristic richness of the recent alpine communities was similar to that of the soil seed-banks for the small plots (10 x 10 cm; Table 5). Thousands of *Gagea glacialis* bulbs were found in GHM and SBC samples (Semenova and Onipchenko 1990).

Annual seed production

We have investigated the density of flowering shoots and number of seeds per shoot for most of the alpine species for 3-5 years. Using these values we estimated the annual seed production. The following species produce about 200 and more seeds per m^2 annually: *Campanula biebersteiniana, Carum caucasicum, Gentiana djimilensis, Primula algida* (all in ALH), *Festuca varia* (only for mast years), *Leontodon hispidus, Gentiana djimilensis, Nardus stricta* (all in FVG), *Anthoxanthum odoratum, Campanula biebersteiniana, Nardus stricta, Veronica gentianoides, Luzula multiflora, Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica* (all in GHM), *Gnaphalium supinum, Pedicularis nordmanniana, Taraxacum stevenii* (all in SBC); (Guzhova, Rabotnova and Onipchenko 1990).

The total seed yield exceeded 1,000, 2,000, 2,000 and 4,000 seeds/m^2 for SBC, ALH, FVG, and GHM resp.

The population strategies of alpine species

Using the data on biomass, seed bank, seed yield, seed weight, reproductive allocation and a response to disturbance we used to determine the population strategies of the species (sensu Ramenskii-Grime concept in Romanovsky interpretation - Romanovsky 1989; Onipchenko *et al.* 1991). The differentiation in strategies in terms of interspecific variation of the above-mentioned parameters was more obvious greater in the FVG and GHM than in the ALH and SBC. Among the investigated species, *Geranium gymnocaulon, Hedysarum caucasicum* and *Festuca varia* had the most expressed properties of a violent (sensu Ramenskii 1938; competitors sensu Grime 1979). *Viola oreades, Vaccinium vitis-idaea, Deschampsia flexuosa* were identified as patients (stress-tolerantors). *Gagea glacialis, Anthoxanthum odoratum, Matricaria caucasica, Gnaphalium supinum, Veronica gentianoides, Gentiana biebersteinii, Sibbaldia procumbens* are explerents (ruderals). The latter group is the most promising for the restoration of the disturbed alpine sites.

Communities dynamics

Seasonal dynamics

The detailed phenological description of the ALH was represented by Onipchenko (1983). This community has a relatively long growing season (more than 5 months). Phenological curves showing the number of species at different phenophases during the time of a year were bell-shaped (Fig. 1). Most of

Fig. 3. The structure of the Alpine Lichen Heath. Plants (from left to right): *Helictotrichon versicolor, Cetraria islandica, Carex umbrosa, Cetraria islandica, Festuca ovina, Plantago saxatilis* (from Onipchenko 1985).

Variant	Vascular plants biomass			Lichen biomass		
	1981	1983	sign.	1981	1983	sign.
Control	119±9	133±11	ns	270±30	279±44	ns
N	173±16	199±19	ns	234±36	233±27	ns
NK	157±26	238±13	$p<0.05$	237±30	208±25	ns
NK	244±24	367±43	$p<0.05$	151±33	111±28	ns
NPK	232±22	335±41	$p<0.05$	274±39	187±48	ns

Table 6. The aboveground biomass of the vascular plants and lichens during 3 years of a fertilization experiment (g/m^2, average ± s.e., n = 10). The nutrients were added in May 1981, May 1982 and May 1983, the biomass was estimated in August each year.

the species are deciduous, but some dominants *(Festuca ovina, Carex sempervirens, Carex umbrosa)* have partly wintergreen leaves as well. Because of high irradiation and thin snow cover, netto-assimilation of lichens can take place in the midwinter (see Fig. 2 for temperature pattern). Other types of the alpine communities (FVG, GHM and SBC) have a shorter growing period and similar bell-shaped phenological curves (Onipchenko and Ustinova 1993).

Fluctuations

We investigated fluctuations from year to year of shoot density in permanent plots. For some species we have made observations of individual plant development for 12 years.

The density of vegetative shoots of most of the alpine species have changed slightly from year to year, but the density of generative shoots show great fluctuations for the same period of time (Onipchenko 1987). Because of negligible changes of structure and composition, the investigated communities can be regarded as stable-fluctuated following Rabotnov (1983).

The observation of some individuals of *Anemone speciosa, Carum caucasicum, Campanula biebersteiniana* confirmed the ideas of a prolonged longevity of alpine plants (Rabotnov 1950; Bliss 1971). The juvenile phase of these species can last for more than 10 years. Most adult individuals of these species did not produce flowers every year; the break in flowering can last for 3-5 years and more for some individuals.

Successions of the alpine communities during Holocene

The radiocarbon age of the humic acids (the first fraction) was determined for the lower soil horizons as 3,630±60, 2,950±80 and 3,610±80 years for the SBC, GHM, and FVG resp. (Grishina *et al.* 1987). We can suggest that the vegetation development has started at least in the middle of the Holocene.

The recent pollen depositions were investigated for the main types of alpine communities. *Poaceae* - pollen was the main group of pollen in the FVG, *Geranium* pollen characterized pollen diagrams of the GHM. The proportion of alien pollen of trees *(Pinus, Betula* etc.) decreased rapidly from ALH to SBC pollen diagrams (Pavlova and Onipchenko 1992).

Using pollen analysis of alpine soils we investigated the basic tendencies of successions for the second half of the Holocene (Pavlova and Onipchenko 1992). Occupying the upper parts of geochemical catenas (toposequences) the ALH and FVG were very stable during the last millennium. On the contrary, a thousand years ago more xeric communities occupied areas which are now covered by GHM and SBC. This change could be due to changes of snow depth in small depressions during the second half of the Holocene.

Experimental investigation of the ALH community structure

Relationships between lichens and vascular plants

The stands of the ALH have the specific spatial structure: small lichen patches (up to 10 cm across) alternate with graminoid bunches *(Festuca ovina, Carex sempervirens, C.umbrosa)* or isolated shoots of vascular plants. Pure lichen or vascular plants patches with diameters of more than 20 cm across are absent from this community. There is a significant amount of thin roots in the soil under lichen patches (Fig. 3). The following hypothesis was suggested to explain this pattern (Onipchenko 1984):

The ALH-soils are relatively nutrient-poor and shallow. Thus the vascular plants are forced to develop large root systems. We suppose that the root systems occupy larger area than necessary for the aboveground shoots. So the open patches without live shoots (gaps) can be left at the aboveground level of vascular plants. Fruticose lichens can occupy these patches, because they receive the main nutrients from precipitation and atmospheric dust. The lichens make up the main part of aboveground phytomass (Table 3), but they cannot compete efficiently with vascular plants for soil nutrients. Vascular plants form the "framework" of the community. Because of strong winds, the fruticose lichens can not develop without the "framework" of the vascular plants.

Consequences:

(1). Removal of lichens would not change other components of the plant community significantly.

(2). Addition of nutrients (fertilization) should increase aboveground biomass and cover of vascular plants, and decrease biomass of the lichens due to competition for light.

(3). Root cutting under lichen patches should facilitate the settlement and growth of vascular plants on these patches in comparison with control (non cutted) areas.

A series of experiments was carried out to test these predictions (Onipchenko 1984, 1985).

Lichen removal experiments

The fruticose lichens were carefully removed from four 1 m^2 plots. Density of shoots on 16 small plots (25 x 25 cm) have been estimated for 10 years. The density of shoots was compared with initial data and with the data for control plots. There was no significant change of shoot density for most of the vascular species after the lichens removal. Only the densities of semiparasitic *Euphrasia ossica*, evergreen *Vaccinium vitis-idaea*, and young genets of *Carum caucasicum* have increased. The barren areas (on lichen sites) neither have not diminish nor they have been overgrown. Sometimes soil surface disturbance due to frost action took place in these microsites.

Fertilization experiments

Experiments with nutrient additions (variants: Ca, N, P, K, PK, NK, NP, NPK; rates of fertilization: Ca 900, N 90, P 60, K 60 kg $^{-1}$ha $^{-1}$) had been carried out for 3 years. Significant changes of vascular plant biomass and composition were found only in variants where N was added (Table 6). The lichen biomass slightly decreased on variants NP and NPK, but the changes between 1981 and 1983 year were not significant. Vascular plants formed a dense cover in these variants. It seems that 3 years is too short a period for obvious lichen-cover degradation because of the slow rate of lichen decomposition in the community (Voronina, Onipchenko and Ignat'eva 1986). Significant decrease of the lichen biomass was obtained when we compared the average values in control plots for three years (275 g/m^2 , n=30, st.er.=22) and average values in all N-variants in 1983 (185 g/m^2, n=40, st.er.=17, $p<0.01$).

The root-cutting experiments

The soil under lichen patches was isolated from neighbour vascular plant roots using metallic tubes (diameter 7 or 10 cm, depth 8-10 cm, 12 replications).

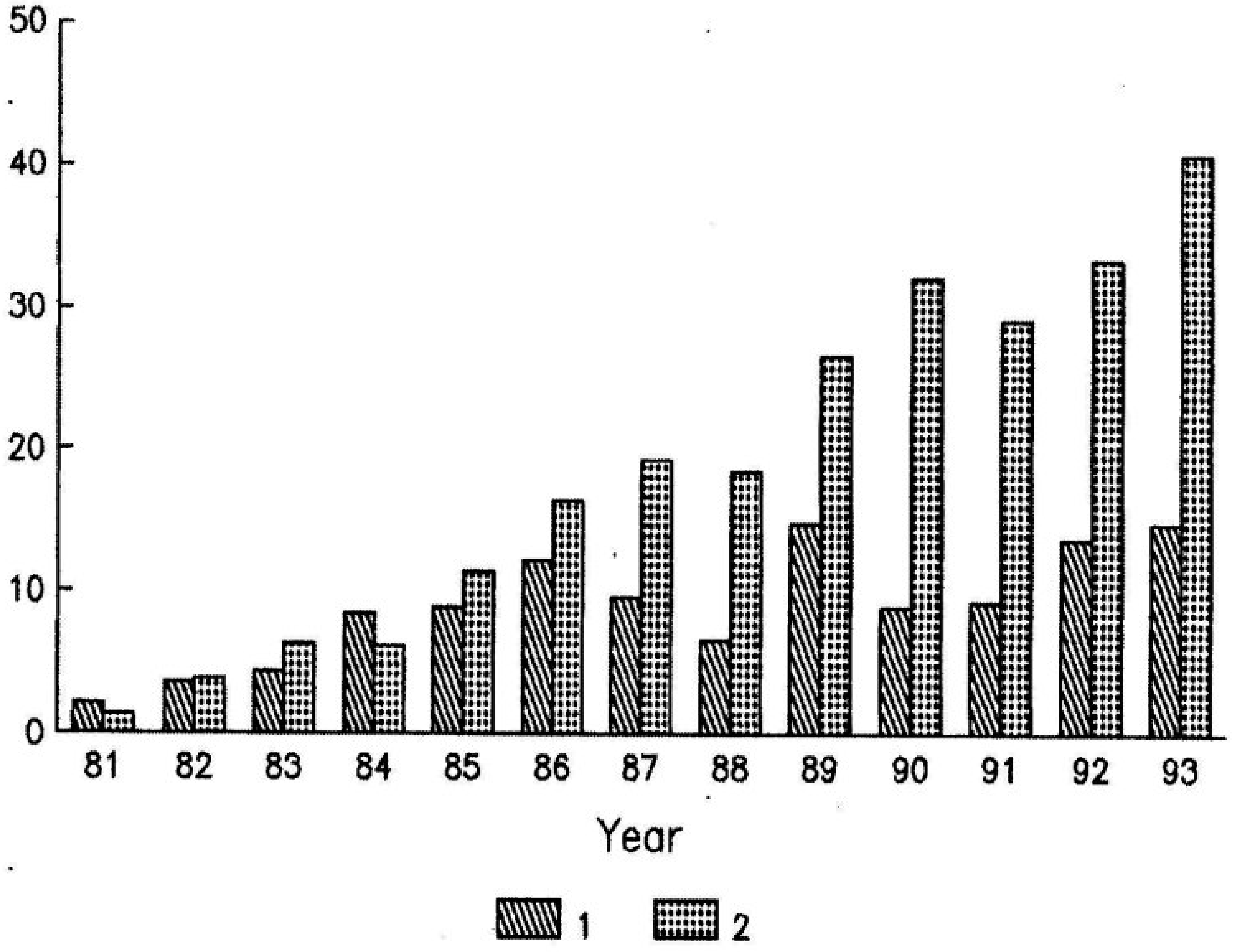

Fig. 4. The sum density of shoots and seedlings for all vascular plants (number per dm^2) on experimental (1), and control (2) plots of the Alpine Lichen Heath during 11 years after root-cutting experiment.

Variant of experiment	Date of observation (month/year)			
	6.86	8.86	8.87	8.88
Control	29(5) -------- 14.8±0.2	29(19) --------- 17.3±0.2	29(13) ------- 17.1±0.2	30(15) --------- 17.4±0.2
Shading for the 1st half of vegetative season	25(11) -------- 13.9±0.2	21(4) ------- 11.8±0.3	21(2) ------- 10.8±0.2	20(4) ------- 10.7±0.2
Shading for the 2nd half of vegetative season	25(15) -------- 15.5±0.2	22(11) -------- 13.0±0.2	22(8) -------- 13.6±0.2	21(5) -------- 12.5±0.3
Shading for 3 months	27(11) -------- 14.0±0.1	18(2) ------- 8.0±0.2	7(0) ------- 2.6±0.1	7(0) -------- 2.6±0.2

Table 7. Floristic richness of the alpine lichen heath during the shading experiments (from Rabotnova, Onipchenko and Ustinova 1992). Above line - total species number for all experimental plots, number of species with generative shoots (in parenthesis), below line - average species number per plot (25x25 cm)±standard error, n=10.

The tubes were left in the soil to prevent lateral root growth. We have counted the number of shoots and seedlings at the end of each growing season during 13 years. The number of shoots and seedlings on the experimental plots have slowly increased (Fig. 4). Significant differences as compared to the control plots were obtained only after 10 years.

As a whole, the results of all our experiments have do not contradict the hypothesis about coenotic mechanisms forming the ALH-pattern (Onipchenko 1984, 1985). Grabherr (1989) suggested similar ideas to explain patterns in the alpine sedge grassland (Caricetum curvulae).

Experiments with artificial shading

The competition ability of alpine species for light was investigated using experiments with artificial shading. We estimated the ability of phenological divergence among alpine plants and their tolerance to light deficit. Screens of textile fabric were used. They had a high permeability for water, but absorbed and reflected about 95% of the solar radiation on cloudless days. There were 4 treatments of the experiment: control, shading for 1.5 month during the first half of the vegetation season, shading for 1.5 month during the second part and shading for the whole summer (3 months). The experiment lasted 3 years. The results were summarized by Rabotnova, Onipchenko and Ustinova (1992) and are presented here in a brief form:

(1) Most alpine species assimilate during the whole vegetative season; no significant phenological differentiation between species was found.

(2) The shading for 3 months during 3 years had a strong impact on structure and composition of the community. The shoot density of all species drastically decreased and most of the species disappeared from the community (Table 7). Evergreen species such as *Vaccinium vitis-idaea, Gentiana djimilensis, G. oschtenica* were the most shade-tolerant.

(3) The shoot density of most of the species had decreased as a result of the shading for 1.5 month. A compensatory increase in shoot number was not found in any species. The species most sensitive to shading included *Luzula spicata, Euphrasia ossica, Minuartia circassica, Arenaria lychnidea. Helictotrichon versicolor* was sensitive only to shading for the first half of summer.

(4) The experimental shading caused a higher decrease of generative shoots than of vegetative ones. Most of the species in the ALH did not produce generative shoots after shading. This could be the cause of their poor competitive ability in more dense and tall-grown alpine grasslands and meadows.

Conclusions

The results of the first stage of this long-term ecological research allow to conclude that the composition and the structure differ considerably among the communities within the alpine zone. The following factors are the most significant for the investigated communities:

- the absence of snow cover and lack of nutrients in the alpine lichen heath;
- relatively favorable hydrothermic conditions and animal burrowing activity in the alpine grasslands and meadows;
- a great snow accumulation and short vegetative season for snow bed communities.

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