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. Seed and seed banks in meadows and snow bed communities are greater than in grasslands and lichen heaths. Most of the alpine species (77%) have mycorrhiza. Vascular-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 fruitlose 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; Shimada 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 researchers 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 Hatpara, Teberda Reserve, Karachai, the NW Caucasus, Russia 43° 16' N, 41° 41' E; altitude: 2,700 - 2,800 m.

A crena (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 (GHMC) and Alpine Snow Bed communities (SBC). The taxonomic families of the examined plots are presented in Table 1. Syntaxonomic follows Onipchenko, Mineeva and Rabotnova (1987), Onipchenko et al. (1992), the data on floristic richness are compiled from Onipchenko and Semenova (1989).

See Appendix 1 for vascular plant nomenclature.

(1) The alpine lichen heath is dominated by fruitlose lichens (mostly Cladina islandica). This type, belonging to the Pediculari chrozophytae-Britischietum caucasicz Mineeva 1987 (Juncetum 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 biaristitsiana, Anemone sacchara and Antennaria dioica are the dominant vascular plant species forming more than 5% of the aboveground biomass.

(2) The Festuca varia grassland (Viola oradis-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 46.6 species per plots of

<table>
<thead>
<tr>
<th>Community type</th>
<th>ALH</th>
<th>FVG</th>
<th>GHM</th>
<th>SBC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relief forms</td>
<td>crests, ridges, windward slopes</td>
<td>slopes (often steep)</td>
<td>leeward slopes &amp; small depressions</td>
<td>bottoms of deep depressions</td>
</tr>
<tr>
<td>Depth of snow cover in winter (m)</td>
<td>0.0-0.3</td>
<td>0.5-1.5</td>
<td>2.0-4</td>
<td>5 and more</td>
</tr>
<tr>
<td>End of snow melting</td>
<td>April/May</td>
<td>end of May/first half of June</td>
<td>June/first half of July</td>
<td>July/first half of August</td>
</tr>
<tr>
<td>Duration of vegetation period (months)</td>
<td>4.5-5.5</td>
<td>3.5-4.5</td>
<td>2.5-3.5</td>
<td>1.5-2.5</td>
</tr>
<tr>
<td>Aspect</td>
<td>S</td>
<td>SSW</td>
<td>SW</td>
<td>SW</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>15</td>
<td>10</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Number of the vole burrows per hectare (average ± s.e., n=25)</td>
<td>300±110</td>
<td>1500±290</td>
<td>3700±590</td>
<td>30±30</td>
</tr>
</tbody>
</table>

26 × 25 cm and 5 × 5 m, resp.). Festuca varia and Nardus stricta are dominants.

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

4) The alpine carpet-like snow-bed communities of the Hyllopo ponticas-Pediculatetum nordmannianae (Rabotnova 1997), Salicetea herbacea, occupy depressions. Short rosette and dwarf-trailing plants, such as Siberidia procumbens, Taraxacum stenenti, Glaucium supinum Minuartia acaulis, and tussocky Nardus stricta are the dominants. The floristic richness is 7.9 and 18.0 species per plots of 25 × 25 cm and 5 × 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 Corydthetum 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 Pas 1971; Müller 1987). Some characteristics of the soils are represented in Table 2. A more detailed description of the soils is given in Cratina et al. (1993). The burrowing activity of pine voles (Phymys major 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, 6 - Bacillariophyta, and 6 - Xanthophyta). The biomass of algae attained 1.2-1.6 g of fresh weight/m² (Leinsoo, Onipchenko and Shitina 1987). Fewer algae species were found in the GHM and the SBC (Shitina, personal communication).

Lichens

Epiglous 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(NH₄Cl) & 1.2 & 3.2 & 4.2 & 6.1 \\
P & 0.6 & 0.5 & 0.8 & 0.7 \\
K & 29 & 19 & 31 & 61 \\

<table>
<thead>
<tr>
<th>Community</th>
<th>ALH</th>
<th>FVG</th>
<th>GHM</th>
<th>SBC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground phytomass (n=60):</td>
<td>113±7</td>
<td>306±17</td>
<td>318±20</td>
<td>126±5</td>
</tr>
<tr>
<td>vascular plants</td>
<td>440±23</td>
<td>38±2</td>
<td>6±3</td>
<td>2±1</td>
</tr>
<tr>
<td>lichens</td>
<td>3±3</td>
<td>9±2</td>
<td>2±2</td>
<td>3±1</td>
</tr>
<tr>
<td>mosses</td>
<td>229±17</td>
<td>90±104</td>
<td>200±17</td>
<td>156±28</td>
</tr>
<tr>
<td>litter nécromass</td>
<td>478±42</td>
<td>636±34</td>
<td>1392±177</td>
<td>944±128</td>
</tr>
<tr>
<td>Biomass</td>
<td>403±38</td>
<td>565±46</td>
<td>4910±49</td>
<td>592±38</td>
</tr>
</tbody>
</table>

120 alpine vascular plant species were investigated for mycorrhiza. Vascular-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 kareliniana, 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 nécromass 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 (Lotiesov et al. 1991). The belowground phytomass (biomass + nécromass) was the highest in GHM (about 1,900 g/m²). The belowground biomass was three times as much as nécromass in this community. In the other investigated communities belowground biomass only slightly exceeded the nécromass.

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

**Table 2.** Selected soil properties of the alpine communities (from Onipchenko, Vanjass and Selensneva 1988; Griesnas et al., 1993).

The AhL, Cetraria islandica, is dominating by its biomass of 230-450 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 Štefánd Reserve (Gfattova, Váša 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.

**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.
productivity decreased in snow-free communities with deep soil freezing as well as in snow-bed communities with a short growing season (Onipchenko 1980).

Specific features of the biological turnover were investigated for ALH (Vorontsova, Onipchenko and Ignateva 1988). Si, Ca, N, and P are the prevailing mineral elements occurring in the phytomass. The turnover is slow, and the period of litterfall decomposition exceeds 20 years. Thus, the biological turnover has properties similar to those of the alpine tundra ecosystems and grasslands (Ignateenko and Berman 1978; Tiltianova 1973; Basilevich 1984; Vorontsova, Onipchenko and Ignateva 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 1959): Anemone s. s., Campanula biebersteiniana, Festuca varia, Fr. brunnescens and Geranium gymnocalion. 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, Hedyranthus 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 1980, 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, 2,470-5,230 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

<table>
<thead>
<tr>
<th>Species</th>
<th>ALH</th>
<th>FVG</th>
<th>GHM</th>
<th>SBC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthoxanthum odoratum</td>
<td>0</td>
<td>20±9</td>
<td>155±61</td>
<td>5±5</td>
</tr>
<tr>
<td>Carex arata</td>
<td>0</td>
<td>170±42</td>
<td>75±20</td>
<td>45±21</td>
</tr>
<tr>
<td>Carex creperula</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>35±13</td>
</tr>
<tr>
<td>Carex umbrosa</td>
<td>25±5</td>
<td>5±5</td>
<td>10±7</td>
<td>0</td>
</tr>
<tr>
<td>Cerastium purpurascens</td>
<td>0</td>
<td>100±61</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Euphrasia osika</td>
<td>0</td>
<td>100±63</td>
<td>10±10</td>
<td>0</td>
</tr>
<tr>
<td>Festuca ovina</td>
<td>15±15</td>
<td>75±55</td>
<td>20±8</td>
<td>10±7</td>
</tr>
<tr>
<td>Festuca varia</td>
<td>0</td>
<td>5±5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gentiana dalmatica</td>
<td>40±20</td>
<td>10±10</td>
<td>0</td>
<td>1475±333</td>
</tr>
<tr>
<td>Geranium gymnocalion</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gnaphalium supinum</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hedyranthus caucasicum</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Luzula multiflora</td>
<td>0</td>
<td>20±16</td>
<td>1800±406</td>
<td>90±61</td>
</tr>
<tr>
<td>Matricaria caucasia</td>
<td>0</td>
<td>0</td>
<td>1190±196</td>
<td>25±12</td>
</tr>
<tr>
<td>Nardus stricta</td>
<td>0</td>
<td>455±190</td>
<td>210±58</td>
<td>20±12</td>
</tr>
<tr>
<td>Phleum alpinum</td>
<td>0</td>
<td>0</td>
<td>175±82</td>
<td>10±7</td>
</tr>
<tr>
<td>Sibbaldia procumbens</td>
<td>0</td>
<td>0</td>
<td>110±38</td>
<td>765±187</td>
</tr>
<tr>
<td>Taraxacum stevenii</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>245±115</td>
</tr>
<tr>
<td>Veronica gentianoides</td>
<td>45±45</td>
<td>25±12</td>
<td>160±71</td>
<td>5±5</td>
</tr>
</tbody>
</table>

Sum (seeds)  350±180  1190±194  3860±481  2310±422
Gagea glacialis (bulbs)  0  510±193  2940±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).

<table>
<thead>
<tr>
<th>Community</th>
<th>species richness</th>
<th>seed bank</th>
</tr>
</thead>
<tbody>
<tr>
<td>FVG</td>
<td>4.6±0.6</td>
<td>3.7±0.4</td>
</tr>
<tr>
<td>GHM</td>
<td>5.3±0.5</td>
<td>5.4±0.4</td>
</tr>
<tr>
<td>SBC</td>
<td>5.1±0.3</td>
<td>4.2±0.4</td>
</tr>
</tbody>
</table>

**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 gymnocauleon, Hedyarum 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/m²) 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 Cagaea glacialis bulbs were found in GHM and SBC samples (Semionova 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 m² annually: Campanula biebersteiniana, Geum caucasicum, Gentiana diamilensis, Primula algida (all in ALH), Festuca varia (only for most years), Leontodon hispichus, Gentiana diamilensis, Nardus stricta (all in FVG), Anthoxanthum odoratum, Campanula biebersteiniana, Nardus stricta, Veronica gentianoides, Luzula multiflora, Geranium gymnocauleon, Hedyarum caucasicum, Matricaria caucasic (all in GHM). Gnaeffium 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/m² for SBC, ALH, FVG, and GHM resp.

The population strategies of alpine species

Using the data on biomass, seed bank, seed yield, weight, reproductive allocation and a response to disturbance we used to determine the population strategy 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 gymnocauleon, Hedyarum caucasicum and Festuca varia had the most expressed properties of a violent (sensu Ramenskii 1983; competitors sensu Grime 1979). Viola godeae, Vaccinium vitis-idaea, Deschampsia flexuosa were identified as patients (stress-tolerators). Cagaea glacialis, Anthoxanthum odoratum, Matricaria caucasic, Gnaeffium supinum, Veronica gentianoides, Gentiana bieberstein, Sibbaldia procumbens are exliberants (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 (1963). 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): Helototrichon versicolor, Cetraria islandica, Carex umbrosa. Cetraria islandica, Festuca ovina, Plantago saxatilis (from Onipchenko 1965).
Table 6. The aboveground biomass of the vascular plants and lichens during 3 years of a fertilization experiment (g/m², 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.

<table>
<thead>
<tr>
<th>Variant</th>
<th>Vascular plants biomass</th>
<th>Lichen biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>119±9</td>
<td>133±11</td>
</tr>
<tr>
<td>N</td>
<td>173±16</td>
<td>199±19</td>
</tr>
<tr>
<td>NK</td>
<td>157±26</td>
<td>238±13</td>
</tr>
<tr>
<td>NK</td>
<td>244±24</td>
<td>367±43</td>
</tr>
<tr>
<td>NPK</td>
<td>232±22</td>
<td>335±41</td>
</tr>
</tbody>
</table>

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 (1963).

The observation of some individuals of Anemone speciosa, Carum caucasicum, Campanula biebersteiniana confirmed the ideas of a prolonged longevity of alpine plants (Rabotnov 1960, Blute 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±90 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 2), 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-cut) 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 m² 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 oessica*, 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 500, N 90, P 60, K 60 kg 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 5). 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 (278 g/m², n=30, st.err.=22) and average values in all N-variants in 1983 (185 g/m², n=40, st.err.=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).

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**Fig. 4.** The sum density of shoots and seedlings for all vascular plants (number per dm²) on experimental (1), and control (2) plots of the Alpine Lichen Heath during 11 years after root-cutting experiment.
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 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 (Carex curvula).

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 translucent 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 (8 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 djamalensis, G. ochroleuca 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 spica, Euphrasia ostii, Minuartia circassica, Arenaria lychneoides. Helicotrichon 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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