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Autor: Onipchenko, Vladimir G. / Blinnikov, Mikhail S. / Sennov, Andrej V.

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

Vladimir G. ONIPCHENKO

8.1. INTRODUCTION

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

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

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

Accepting this hypothesis, the following assumptions can be attempted:

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

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

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

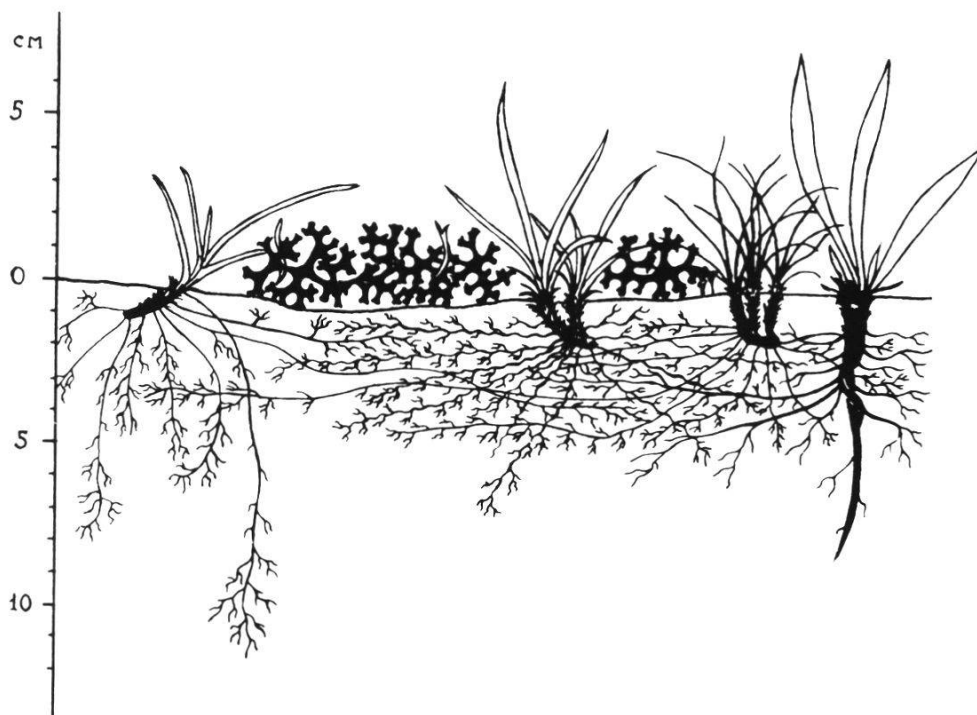


Fig. 8.1. The structure of alpine lichen heath. Plants (from left to right): *Helictotrichon versicolor*, *Cetraria islandica*, *Carex umbrosa*, *Cetraria islandica*, *Festuca ovina*, *Plantago saxatilis* (from ONIPCHENKO 1985).

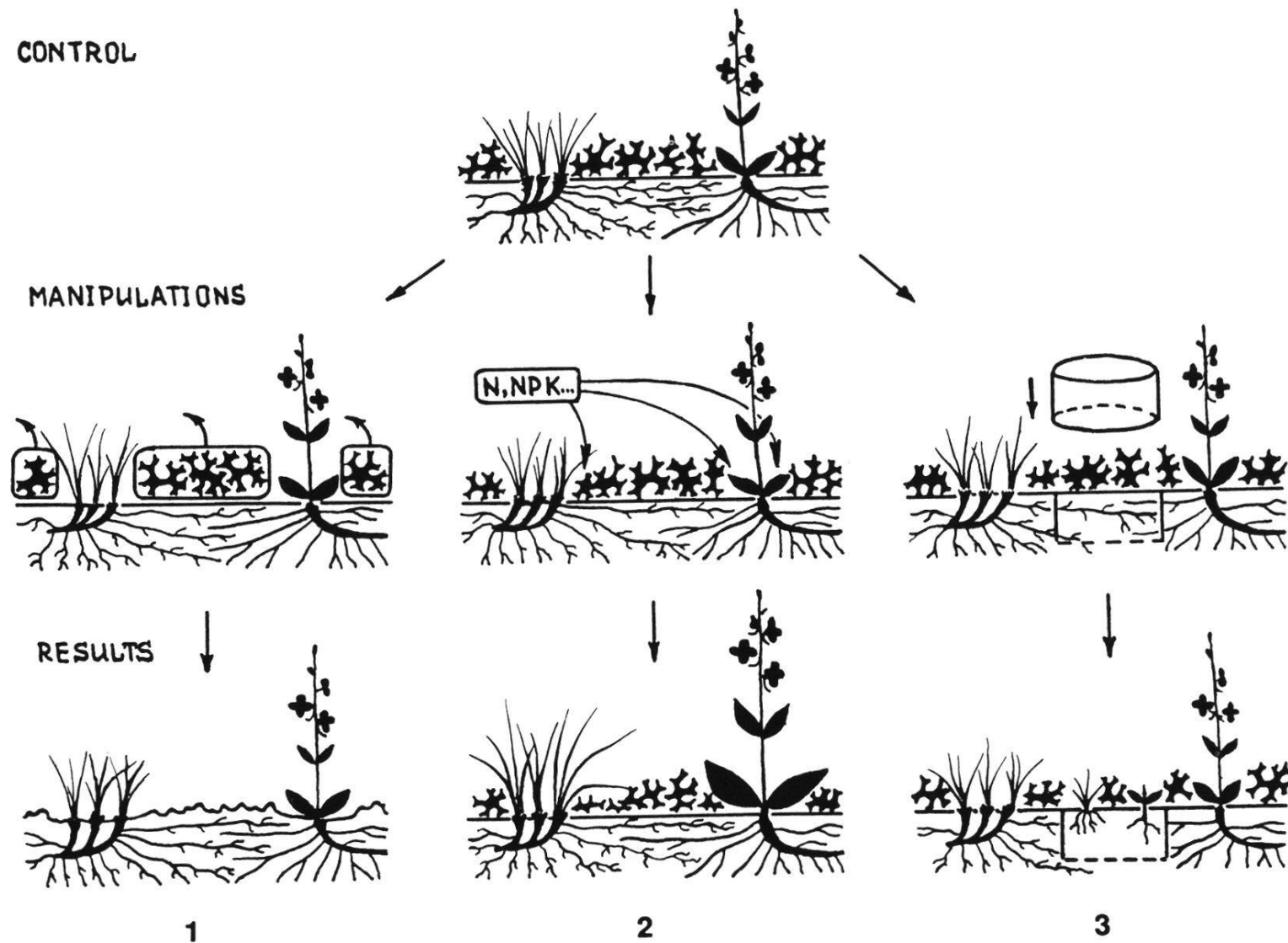


Fig. 8.2. Schematic diagram of experiments: 1 = lichen removal experiment, 2 = fertilization, 3 = root cutting.

8.2. METHODS

8.2.1. Lichen removal experiments

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

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

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

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

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

8.2.2. Fertilization experiments

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

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

8.2.3. Root cutting experiments

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

8.3. RESULTS AND DISCUSSION

8.3.1. Lichen removal experiments

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

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

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

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

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

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

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

8.3.2. Fertilization experiments

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

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

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

Table 8.1. Vascular plant shoot density on control plots and plots cleared of lichens during 12 years (number of shoots per sq.m).

t-test for differences between mean values for first and last 5 years intervals: *** $p > 0.999$, ** $p > 0.99$, * $p > 0.95$. Shoot number for *Festuca ovina* and *Vaccinium vitis-idaea* is bound to multiply by 10.

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

Table 8.1. (continued)

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

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

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

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

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

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

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

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

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

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

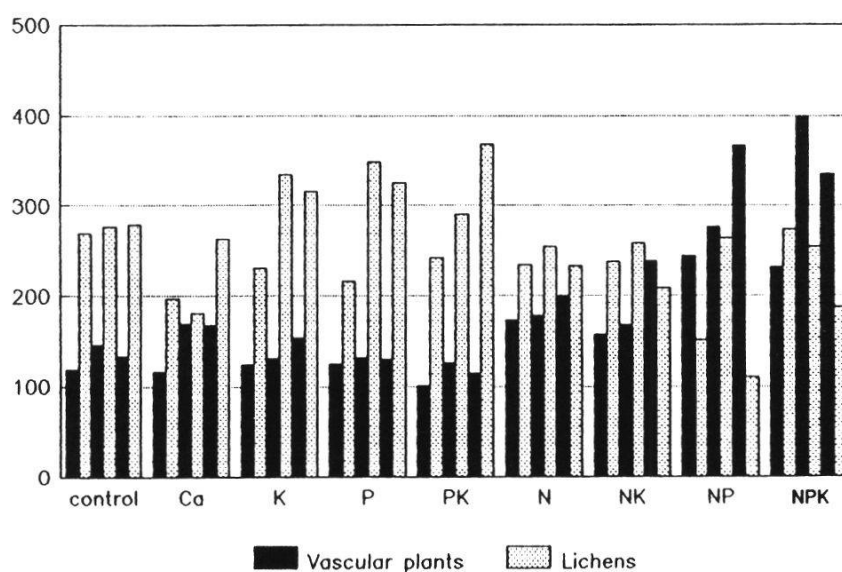


Fig. 8.3. Vascular plant and lichen biomass dynamics during 3 years of fertilization experiment. The first pair of bars in the each variant stand for 1981 values, the second for 1982 and the last for 1983 (g per m², dry mass).

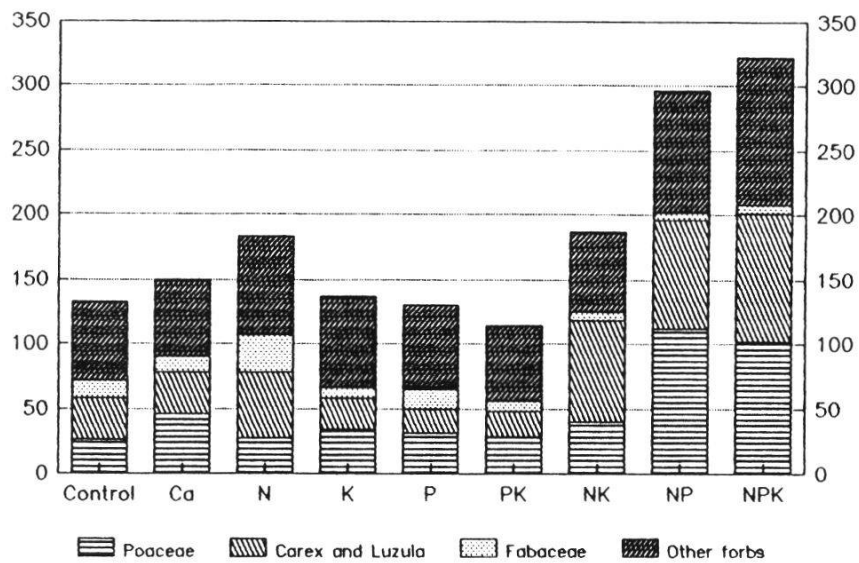


Fig. 8.4. Average vascular plant biomass composition in different variants of the fertilization experiment (g per m², dry mass).

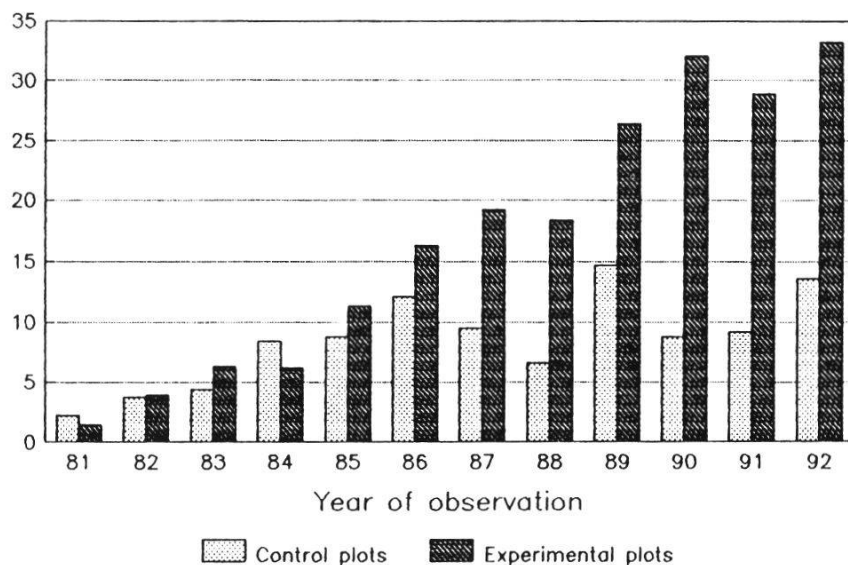


Fig. 8.5. The sum density of shoots and seedlings (average number per dm²) on experimental plots with root cutting (1) and on the control (2) for 12 years.

8.3.3. Root cutting experiments

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

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

SUMMARY

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

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

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

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