Zeitschrift: Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich

Herausgeber: Geobotanisches Institut, Stiftung Rübel (Zürich)

Band: 115 (1994)

Artikel: Experimental investigation of alpine plant communities in the Northwestern Caucasus

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Kapitel: 5: Soil seed banks

DOI: https://doi.org/10.5169/seals-308979

5. Soil seed banks

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5.1. INTRODUCTION

Information about alpine soil seed banks is very scarce (ARCHIBOLD 1984, MORIN and PAYETTE 1988, MCGROW and VAVREK 1989, HATT 1991), especially from the Caucasus (ZIROJAN 1988, GOGINA 1960). The main aim of the present research was to obtain comparative data on soil seed bank features of different alpine communities in Teberda State Reserve in the Northwestern Caucasus. The attempt was made to obtain several characteristics of seed banks, namely total number of germinable seeds, floristic composition and species diversity, spatial distribution, temporal pattern of germination, etc. These parameters can enable an appraisal of the restoration ability of studied communities after disturbances.

Acknowledgement
The authors thank A. Sennov, T. Pochatkova, T. Ulyanova, M. Makarov and N. Nedbaev for the manifold help in greenhouse experiments.

5.2. MATERIALS AND METHODS

Soil seed banks were studied in eight alpine plant communities: alpine lichen heaths (ALH), *Festuca varia* dominated grasslands (FVG), *Geranium-Hedysarum* dominated meadows (GHM), snow bed communities (SBC), *Rhododendron caucasicum* bush communities (RCB), alpine bogs (BOG) and open communities on dry and moist screes (DSC and MSC respectively). Their description is given in chapter 1 of this volume. The following fourteen sample areas were studied: ALH(U), ALH(L), FVG(U), FVG(L), GHM(U), GHM(L), SBC(U), SBC(L), RCB(U), RCB(L), BOG(1), BOG(2), DSC and MSC.
Ten soil samples 10x10x10 cm were taken from each sample area. Each

sample was divided into 2 cm-thick layers, air dried, packed and transported to the greenhouse of Moscow State University (Moscow). The samples from dry and moist screes were divided into 5 cm-thick layers, because soils of these habitats were very stony, complicating their division.

Dry samples were spread out on sterilized sand in the greenhouse and watered. We counted germinated seedlings and removed them after identification. The seedlings which we could not identify were planted and grown until they became identifiable.

Samples were taken in July-August, before seed-shedding but after complete seed germination. Therefore, it was attempted to examine only the persistent seed bank (FENNER 1985). Samples were taken in ALH in 1982 (RABOTNOV 1987), in FVG, GHM and SBC in 1986 and in RCB, BOG and screes in 1989. In the greenhouse experiment, the germination process was allowed to occur during 3-4 months in both spring and autumn, it was discontinued during summer and winter for three years of the study. We kept the samples frozen in winter to stimulate seed germination. EBERSOLE (1989) demonstrated that stratification of tundra soils tended to cause germination of a greater number of taxa.

Soil of FVG was collected for the second time in 1989 to test for differences in seed accumulation between *Festuca varia* sods and intersod space. Ten blocks, 10x10 cm, were cut to the depth of 5 cm from *Festuca varia* sods (five samples from each sample area), and ten blocks were similarly sampled from the intersod space.

The four studied communities (ALH, FVG, GHM and SBC) were additionally examined in field experiments. For this purpose five small plots of 500 cm^2 each were chosen in each study area (10 for each community type). The plots were fenced in by metallic hoops set 3-5 cm into the soil. The soil within the fence was ploughed and cleared of plants. To prevent seed loss, large roots, rhizomes and bulbs were washed in water which was then used to water corresponding plots. The plots were watered once or twice per week. To decrease seed invasion we removed all reproductive shoots closer than 0.5 m and covered the plots with a fine net. The net also protected the seedlings from strong light and prevented their being eaten by grasshoppers. Seedlings were counted every week and were removed when identifiable.

The field experiment began in early August, 1988. Observations were made till September and were continued during the next vegetation season. Unfortunately, there was no sense in continuing the experiment in subsequent years because, in spite of protection, seed invasion was considerable.

5.3. RESULTS AND DISCUSSION

5.3.1. Size of alpine seed banks

Soil seed bank composition of studied plant communities is presented in Tables 5.1 and 5.2. Results of seed bank investigations in ALH, FVG, GHM and SBC have already been published in more detail (SEMENOVA and ONIPCHENKO 1990, 1991).

The highest amount of viable seeds per m^2 was found in the soils of BOG (10675 seeds) and MSC (8080 seeds), and lowest in soils of FVG (1190 seeds) and ALH (350 seeds). Intermediate values were found for soils of GHM (3850 seeds), SBC (2810 seeds), DSC (2790 seeds) and RCB (1615 seeds). Thus, the number of germinable seeds in soils increases from dry to moist alpine communities.

These numbers of viable seeds are close to those reported for tundras and polar deserts in many research publications: up to 4000 in Taymyr tundras and from 300 to 700 in polar deserts (HODACHEK 1985), about 2000 in soils of dry tundra and about 150 in moist and hummock tundra in Canada (ARCHIBOLD 1984). Similar values were obtained for alpine meadows on silicate (1607-2291) and dolomite (1386-1455) in Davos, Switzerland (HATT 1991). The amount of viable seeds in different tundra communities in Alaska ranged from 70-600/m^2 (EBERSOLE 1989).

Much fewer seeds were found in alpine tundra soils in Quebec (Canada) (13-144) (MORIN and PAYETTE 1988). However, different methods were applied (washing off on meshes, with consequent germination and testing of viability for nongerminated seeds). ARCHIBOLD (1984) carried out a thorough study of soil seed banks of four alpine soils in the Canadian Rocky Mountains. At the timberline there were 931-1759 seeds/m^2, in a wet bog 10561 seeds/m^2, and in dry alpine meadow soil 20425 seeds/m^2. This data exceeds the present results by several times (except the bog), although it was obtained in early October after seed shed. Soils under *Campanula tridentata*-dominated snow bed communities in Aragaz, Armenia, contain 7600 seeds/m^2 (ZIROJAN 1988), still 2-3 times more than the present findings *Campanula* seeds constituted 78% of total seed bank.

The following data were obtained by means of the field method: ALH 272 seeds/m^2, FVG 108 seeds/m^2, GHM 846 seeds/m^2, and SBC 256 seeds/m^2. These numbers were several times less than the corresponding values of the greenhouse experiment (from 1.3 to 8.8 times in different communities). The

Table 5.1. Soil seed bank composition of 4 alpine community types: a comparison of greenhouse and field experiments (before and after slash respectively, seeds per m^2). ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities.

	community types			
	ALH	FVG	GHM	SBC
Ajuga orientalis	0 / 0	5 / 0	0 / 0	0 / 0
Alchemilla caucasica	4 / 12	5 / 0	0 / 0	5 / 0
Anemone speciosa	7 / 22	0 / 0	0 / 0	0 / 0
Anthoxanthum odoratum	0 / 0	20 / 6	155 / 72	5 / 0
Arenaria lychnidea	4 / 0	0 / 0	0 / 0	0 / 0
Campanula biebersteiniana	11 / 6	5 / 0	5 / 0	0 / 2
Campanula collina	0 / 2	0 / 0	0 / 0	0 / 0
Carex atrata	0 / 0	170 / 2	75 / 24	45 / 12
Carex oreophila	0 / 0	0 / 0	0 / 0	35 / 0
Carex pyrenaica	0 / 0	0 / 0	0 / 0	15 / 6
Carex sempervirens	7 / 14	0 / 0	0 / 0	0 / 0
Carex umbrosa	5 / 20	5 / 8	10 / 0	0 / 0
Carum caucasicum	18 / 36	0 / 0	0 / 0	0 / 0
Carum meifolium	0 / 0	0 / 0	0 / 24	0 / 0
Catabrosella variegata	0 / 0	0 / 0	0 / 0	20 / 16
Cerastium purpurascens	0 / 0	100 / 4	0 / 0	0 / 0
Corydalis conorrhyza	0 / 0	0 / 0	0 / 0	0 /106
Erigeron sp.	0 / 0	0 / 0	0 / 0	5 / 0
Erigeron uniflorus	0 / 6	0 / 0	0 / 0	0 / 0
Eritrichium caucasicum	4 / 0	0 / 0	0 / 0	0 / 0
Euphrasia ossica	0 / 6	100 / 0	10 / 20	0 / 0
Festuca brunnescens	0 / 2	20 / 0	30 / 2	5 / 0
Festuca ovina	11 / 12	75 / 10	20 / 4	10 / 4
Festuca varia	0 / 0	5 / 0	5 / 0	0 / 0
Gentiana aquatica	4 / 0	0 / 0	0 / 0	0 / 0
Gentiana djimilensis	29 / 66	10 / 4	0 / 0	0 / 0
Gentiana septemfida	14 / 0	0 / 0	0 / 0	0 / 0
Gentiana sp.	0 / 20	120 / 0	0 / 0	0 / 0
Gnaphalium supinum	0 / 0	0 / 0	0 / 0	1475 / 16
Helictotrichon versicolor	7 / 0	0 / 0	0 / 0	0 / 0
Juniperus hemisphaerica	0 / 0	0 / 2	0 / 0	0 / 0
Luzula multiflora	0 / 0	20 / 0	1600 / 20	90 / 0
Luzula spicata	4 / 6	0 / 0	0 / 0	0 / 0
Matricaria caucasica	0 / 0	0 / 0	1190 / 200	25 / 0
Minuartia aizoides	0 / 0	0 / 0	5 / 0	5 / 0
Minuartia recurva	0 / 0	5 / 0	5 / 2	0 / 0
Minuartia sp.	0 / 0	5 / 0	0 / 0	0 / 0
Myosotis alpestris	0 / 0	15 / 2	0 / 0	0 / 0
Nardus stricta	0 / 0	455 / 0	210 / 10	20 / 2
Oxytropis kubanensis	22 / 6	0 / 0	0 / 0	0 / 0
Pedicularis chroorrhyncha	0 / 6	0 / 0	0 / 0	0 / 0
Pedicularis nordmanniana	0 / 0	0 / 0	0 / 0	0 / 8
Phleum alpinum	0 / 0	0 / 0	175 / 328	10 / 18
Primula algida	32 / 0	0 / 0	0 / 0	0 / 0
Pulsatilla albana	11 / 0	0 / 0	0 / 0	0 / 0
Ranunculus oreophilus	4 / 10	5 / 48	0 / 2	0 / 0

Table 5.1. (continued)

	community types			
	ALH	FVG	GHM	SBC
Saxifraga moschata	0 / 0	0 / 0	0 / 0	5 / 0
Sedum tenellum	0 / 0	0 / 0	35 / 80	0 / 0
Senecio aurantiacus	0 / 0	5 / 0	0 / 0	0 / 0
Senecio sp.	4 / 0	0 / 0	0 / 0	0 / 0
Senecio taraxacifolius	0 / 0	5 / 0	0 / 0	0 / 0
Sibbaldia procumbens	0 / 0	0 / 0	110 / 34	765 / 48
Taraxacum stevenii	0 / 4	0 / 0	0 / 0	245 / 12
Trifolium polyphyllum	4 / 0	0 / 0	0 / 0	0 / 0
Trifolium spadiceum	0 / 0	0 / 2	0 / 0	0 / 0
Vaccinium vitis-idaea	0 / 2	0 / 0	0 / 0	0 / 0
Veronica gentianoides	32 / 8	25 / 16	150 / 16	5 / 0
Viola oreades	0 / 0	5 / 2	0 / 0	0 / 0
Ericaceae (undeterm.)	0 / 0	0 / 0	10 / 0	0 / 0
Dicotyledons (undeterm.)	76 / 10	0 / 2	20 / 6	5 / 6
Monocotyledons (undeterm.)	0 / 0	5 / 0	30 / 2	15 / 0
Total number of seeds	350 /272	1190 /108	3850 / 846	2810 /256
Fritillaria lutea (bulbs)	4 / 24	0 / 10	0 / 0	0 / 0
Gagea glacialis (bulbs)	0 / 0	510 /276	2840 /1198	990 /404

causes of this phenomenon were discussed earlier (SEMENOVA and ONIPCHENKO 1991).

5.3.2. Seed bank composition

We determined 23 species of vascular plants in the soil seed bank of ALH, 23 species in FVG, 17 in GHM, 19 in SBC, 29 in RCB, 25 in BOG, 18 in MSC and 23 in DSC. Most of them were ordinary species of corresponding plant communities, with a few species from neighbouring plant communities. For example, such alien seeds belonged to *Pulsatilla albana* in ALH, *Saxifraga moschata* and *Veronica gentianoides* in SBC, *Sagina saginoides* in BOG, etc.

The field experiment revealed 20 species in the seed bank of ALH, twelve species in FVG, 15 species in GHM and twelve in SBC. However, the total area of soil samples here was 2.5 times more than that in the greenhouse.

There were many species which germinated in the greenhouse, but not under field conditions (Table 5.1). Most of them were rare in investigated samples, so they could be that they are absent in the samples by chance. Nevertheless,

Table 5.2. Soil seed bank composition of RCB, BOG, MSC and DSC (seeds per m^2). RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

sample areas	RCB(U)	RCB(L)	BOG(1)	BOG(2)	MSC	DSC
Agrostis vinealis	0	10	0	0	0	0
Alchemilla caucasica	0	0	0	0	0	20
Alchemilla sp.	30	0	0	0	0	0
Alchemilla vulgaris aggr.	0	0	2100	10	0	0
Anemone fasciculata	10	0	0	0	0	0
Anemone speciosa	0	0	0	0	0	10
Anthoxanthum odoratum	0	70	10	180	0	0
Anthyllis vulneraria	20	0	0	0	0	70
Briza marcowiczii	0	60	570	0	0	0
Campanula biebersteiniana	60	0	0	0	0	90
Campanula ciliata	0	0	0	0	0	10
Campanula collina	10	0	0	0	0	0
Cardamine uliginosa	0	0	2020	0	0	0
Carex atrata	80	120	20	0	150	0
Carex nigra	0	0	290	30	0	0
Carex pyrenaica	10	160	10	0	960	0
Carex sempervirens	0	0	0	0	0	20
Carex sp.	0	0	10	0	20	0
Carex umbrosa	0	10	0	0	0	0
Carum caucasicum	0	0	20	90	50	10
Carum meifolium	0	10	0	0	0	0
Catabrosella variegata	0	0	0	0	10	0
Cerastium trigynum	0	0	1280	6800	670	0
Cirsium esculentum	10	0	0	0	0	0
Cirsium simplex	0	0	70	0	0	0
Draba hispida	10	0	0	0	0	30
Empetrum nigrum	30	0	0	0	0	0
Epilobium alpinum	0	0	0	10	0	0
Euphrasia ossica	0	0	0	0	10	230
Festuca ovina	0	0	0	0	0	10
Gentiana aquatica	0	0	0	0	0	80
Gentiana djimilensis	0	0	130	470	0	80
Gentiana oschtenica	30	0	0	0	10	170
Gentiana septemfida	0	0	0	0	0	30
Gnaphalium supinum	20	20	0	0	0	0
Hyalopoa pontica	0	0	0	0	40	0
Luzula multiflora	130	1420	4410	760	810	0
Luzula spicata	0	10	0	0	60	710
Matricaria caucasica	0	10	0	0	0	0
Minuartia aizoides	0	0	70	0	0	0
Minuartia circassica	0	0	0	0	0	10
Minuartia recurva	0	0	0	0	0	10
Nardus stricta	0	0	30	0	0	0
Oxytropis kubanensis	0	10	0	10	0	0
Pedicularis chroorrhyncha	0	0	10	0	0	20
Phleum alpinum	10	220	40	0	0	0

Table 5.2. (continued)

sample areas	RCB(U)	RCB(L)	BOG(1)	BOG(2)	MSC	DSC
Phryne huetii	0	0	0	0	720	0
Potentilla gelida	0	0	0	0	0	120
Primula algida	30	0	0	0	0	730
Primula auriculata	0	0	30	10	0	0
Primula ruprechtii	0	0	0	0	0	20
Primula meyeri	10	0	0	0	70	0
Rhododendron caucasicum	10	30	0	0	0	0
Rumex alpestris	0	0	10	0	0	0
Sagina saginoides	0	0	1570	0	0	0
Saxifraga moschata	10	10	0	10	0	0
Saxifraga sibirica	0	0	20	30	4030	0
Sedum tenellum	150	140	0	10	220	10
Sempervivum caucasicum	0	10	0	0	0	0
Sibbaldia procumbens	20	40	90	20	10	0
Taraxacum sp.	0	0	0	0	10	0
Veronica gentianoides	0	0	0	0	20	130
Veronica telephiifolia	0	0	0	0	140	0
Dicotyledons (undeterm.)	50	80	70	30	50	140
Monocotyledons (undeterm.)	10	0	0	0	20	0
Total number of seeds	750	2480	12880	8470	8080	2790
Polygonum viviparum (bulbs)	0	0	80	0	0	0
Saxifraga sibirica (bulbs)	0	0	20	0	160	0

seedlings of *Nardus stricta* (FVG), *Primula algida* (ALH) and *Carex oreophila* (SBC) were numerous under greenhouse conditions, but absent in the field experiment. Simultaneously there were many seedlings of *Corydalis conorhiza, Pedicularis nordmanniana* (SBC) and *Carum meifolium* (GHM) in the field experiment, which did not appear in the greenhouse. It seems that specific conditions are necessary for their germination.

No germinable seeds of some abundant alpine species, such as *Geranium gymnocaulon, Hedysarum caucasicum, Anthemis iberica, Leontodon hispidus, Deschampsia flexuosa, Antennaria dioica*, etc. were found. Most of them had comparatively high seed productivity. The following species predominated in studied seed banks:

- *Sibbaldia procumbens, Gnaphalium supinum, Taraxacum stevenii* in SBC,
- *Luzula multiflora, Matricaria caucasica, Anthoxanthum odoratum, Nardus stricta, Veronica gentianoides, Carex atrata* in GHM,
- *Nardus stricta, Carex atrata* in FVG,
- *Carum caucasicum, Gentiana djimilensis, Primula algida, Veronica gen-*

tianoides in ALH,
- *Cerastium trigynum, Briza marcowiczii, Carex nigra, Cardamine uliginosa, Alchemilla vulgaris* in BOG,
- *Luzula multiflora, Carex atrata, Sedum tenellum* in RBC,
- *Carex pyrenaica, Saxifraga sibirica, Cerastium trigynum, Luzula multiflora, Phryne huetii* in MSC,
- *Primula algida, Luzula spicata* in DSC.

Our data confirm a well-known tendency (RABOTNOV 1983) that species with violent (RAMENSKY 1938) properties, or edificators of plant communities, usually do not accumulate viable seeds in the soil. The main part of the seed bank consists of non-dominant species, which have some features of explerent strategy (*Luzula multiflora, Matricaria caucasica, Veronica gentianoides* and so on).

Most species of ALH, SBC, BOG, MSC and DSC combine, to a certain extent, both explerent and patient strategies, because they grow under abiotic stress conditions (ecotopic patients). A store of their viable seeds may be insignificant, but they retain their germinating ability for a long time (*Sibbaldia procumbens, Gnaphalium supinum, Carex atrata*). On the whole, it can be concluded that there is more correspondence between recent community composition and soil seed banks for communities developing under severe ecological conditions (ALH, DSC, MSC, BOG) than for highly productive communities (FVG, GHM, RCB).

Also it should be noted, that seeds weighing more than 4 mg are practically absent in the seed bank. At the same time, only species with seeds weighing less than 0.7 mg, are presented in the soil store by more than 100 seeds/m^2.

5.3.3. Species diversity

It is often believed that the floristic diversity of seed bank is considerably less than the diversity of the corresponding plant community. However, the sample areas used to estimate these parameters are usually very different, i.e. less than 1 m^2 in the first case and about 100 m^2 in the second case (RABOTNOV 1982).

The average number of plant species on 10x10 cm plots were compared with the average number of species with viable seeds in the same area (Fig. 5.1). It can be concluded, that these values are similar for FVG, GHM, SBC, RCH. The species diversity of the soil seed banks in MSC, DSC and BOG was approximately two times greater than in the present communities. These

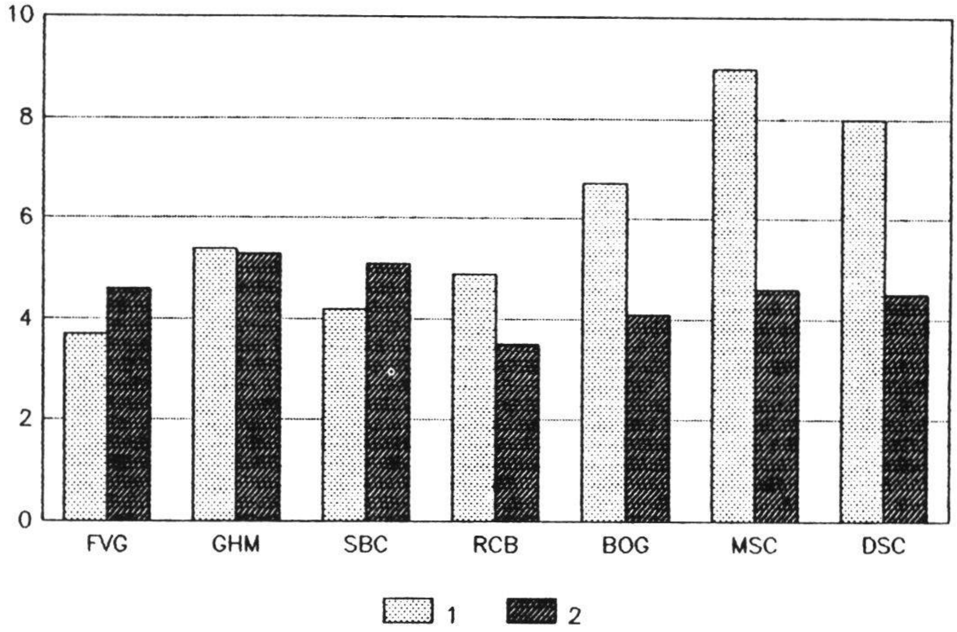

Fig. 5.1. Average number of species (floristic diversity) per 10 x 10 cm plots for soil seed banks (1) and recent plant communities (2).
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities. RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

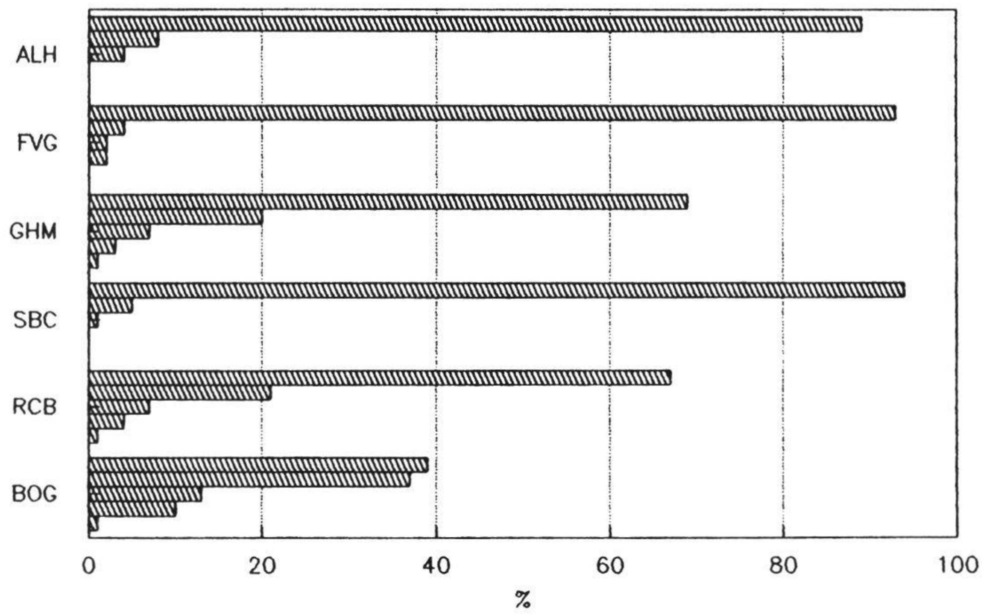

Fig. 5.2. Vertical distribution of viable seeds in 2 cm-soil layers (%) in different communities.
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities. RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs.

differences are reliable using the t-test. It seems that revealing of the entire species composition of a seed bank will require the investigation of larger areas than usual.

5.3.4. Spatial distribution of buried seeds

Most viable seeds are found in the upper 2 cm layer of the soil: ALH 88%, FVG 93%, GHM 70%, SBC 95%, RCB 67%, BOG 39%. Vertical distribution in soil is dissimilar in different communities (Fig. 5.2.).
Soils of DSC and MSC were divided only into two layers with 95% of the seed bank in DSC and 81% in MSC found in the upper layer (0-5 cm) of soil. Buried seeds were discovered to the depth of 10 cm of GHM, BOG and RCB soils. This is probably caused by the intensive burrowing activity of *Pitymys majori* in GHMs and submersion in peat in BOG. Viable seeds were found to the depth of 8 cm in FVG soils, less influenced by *Pitymys majori*, and to the depth of 6 cm in ALH and SBC soils, with negligible zoogenic disturbance.

Table 5.3 Soil seed bank composition of *Festuca varia* sods and intersod space in FVG (number of seeds per 10 plots with total area 0.1 sq. m)

Species	Sods	Intersod space
Ajuga orientalis	0	1
Anthoxanthum odoratum	1	0
Campanula collina	0	1
Carex atrata	27	11
Cerastium purpurascens	3	7
Empetrum nigrum	0	1
Festuca sp.	1	0
Festuca varia	3	10
Gentiana djimilensis	1	0
Gentiana sp.	0	1
Luzula multiflora	1	0
Luzula spicata	1	0
Nardus stricta	1	6
Primula ruprechtii	1	0
Ranunculus oreophilus	2	1
Saxifraga moschata	1	0
Trifolium spadiceum	1	0
Valeriana alpestris	1	0
Veronica gentianoides	1	1
Viola oreades	1	2
Poaceae (undeterm.)	4	0
Total number of seeds	52	42

Seeds weighing less than 0.7 mg can sink deeper into the soils than others. The lower soil layers contain mainly seeds of *Matricaria caucasica, Luzula multiflora, Nardus stricta, Carex atrata, Anthoxanthum odoratum, Cerastium trigynum, Carex pyrenaica, Saxifraga sibirica.*
The horizontal distribution of buried seeds is not homogeneous. The rate of heterogeneity of spatial distribution was estimated according to the variability coefficient values (CV, SD/average value). The following values were obtained for seed banks of different species: *Matricaria caucasica* 74%, *Gnaphalium supinum* 101%, *Sibbaldia procumbens* 109%, *Luzula multiflora* 113%, *Carex atrata* 110-121%, *Veronica gentianoides* 210%, *Phleum alpinum* 210%, *Taraxacum stevenii* 210%. HATT (1991) also found a significant soil bank heterogeneity for alpine meadows near Davos.
Due to a peculiar "tussock" structure of FVG, a difference in seed accumulation could be expected between *Festuca varia* sods and intersod space. However, present observations did not confirm this expectation (Table 5.3.). No significant differences in soil seed bank composition between sod and intersod samples were found. It seems that heavy accumulation of litter can even out the horizontal distribution of seeds in this community.

5.3.5. Dynamics of seed germination

The three year period of observation has allowed the estimation of the seasonal and yearly dynamics of seed germination from the soil samples (Table 5.4.). Seeds of *Nardus stricta, Euphrasia ossica, Taraxacum stevenii, Veronica telephiifolia* and bulbs of *Gagea glacialis* germinated only in spring. Most other seeds germinated mainly in spring. Seedlings of *Matricaria caucasica, Luzula multiflora, Carex pyrenaica, Phryne huetii, Cerastium trigynum, Saxifraga sibirica* and *Phleum alpinum* appeared both in spring and autumn, while seeds of *Festuca ovina* and *Festuca varia* germinated for the most part in the autumn of the first year.
Seedlings of *Nardus stricta, Taraxacum stevenii, Sedum tenellum, Veronica telephiifolia* and *Festuca varia* appeared only in the first year. Seeds of most alpine species germinated mainly in the first year. Seeds of *Gnaphalium supinum, Luzula multiflora, Carex atrata, Alchemilla vulgaris, Briza marcowiczii, Cardamine uliginosa, Carex nigra, Cerastium trigynum, Carex pyrenaica, Phryne huetii, Luzula spicata, Primula algida* and *Euphrasia ossica* germinated during all three years of the experiment. In general, from 68-96% seedlings appeared in different communities during the first year. The highest

Table 5.4. Time of seed germination of some alpine species from soil samples in the greenhouse experiment (number of seedlings for seasons and years).
FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarium caucasicum* meadows, SBC = snow bed communities, RCB = *Rhododendron caucasicum* bush communities, BOG = alpine bogs, MSC = open communities on moist screes, DSC = open communities on dry screes.

Species	seasons		years		
	spring	autumn	first	second	third
FVG					
Carex atrata	34	0	23	3	8
Cerastium purpurascens	19	1	20	0	0
Euphrasia ossica	20	0	10	6	4
Festuca ovina	2	13	13	2	0
Nardus stricta	91	0	91	0	0
Total	219	19	193	30	15
Gagea glacialis (bulbs)	102	0	26	74	2
GHM					
Anthoxanthum odoratum	29	2	27	4	0
Carex atrata	14	1	10	3	2
Luzula multiflora	213	107	198	81	41
Matricaria caucasica	38	100	179	49	10
Nardus stricta	42	0	42	0	0
Phleum alpinum	16	19	34	1	0
Sibbaldia procumbens	21	1	19	3	0
Veronica gentianoides	24	6	23	7	0
Total	519	251	564	151	55
Gagea glacialis (bulbs)	568	0	246	212	110
SBC					
Gnaphalium supinum	272	23	155	97	43
Luzula multiflora	14	4	11	5	2
Sibbaldia procumbens	123	30	85	54	14
Taraxacum stevenii	49	0	49	0	0
Total	495	67	337	165	60
Gagea glacialis (bulbs)	198	0	126	41	31
RCB					
Carex atrata	20	0	18	2	0
Carex pyrenaica	13	4	11	6	0
Luzula multiflora	92	63	136	17	2
Phleum alpinum	1	22	23	0	0
Sedum tenellum	29	0	29	0	0
Total	227	96	284	34	5

Table 5.4. (continued)

Species	seasons		years		
	spring	autumn	first	second	third
BOG					
Alchemilla vulgaris	203	8	172	37	2
Anthoxanthum odoratum	14	5	18	1	0
Briza marcowiczii	44	13	44	11	2
Cardamine uliginosa	172	26	196	4	2
Carex nigra	31	1	23	7	2
Cerastium trigynum	267	541	787	20	1
Gentiana djimilensis	60	0	60	0	0
Luzula multiflora	383	134	371	138	8
Sagina saginoides	139	18	133	24	0
Total	1370	765	1862	256	17
MSC					
Carex atrata	15	0	11	3	1
Carex pyrenaica	28	68	91	4	1
Cerastium trigynum	25	42	65	1	1
Luzula multiflora	22	59	75	5	1
Phryne huetii	27	45	69	2	1
Saxifraga sibirica	44	359	398	5	0
Sedum tenellum	22	0	22	0	0
Veronica telephiifolia	14	0	14	0	0
Total	229	579	778	23	7
DSC					
Euphrasia ossica	23	0	16	7	0
Gentiana oschtenica	17	0	14	3	0
Luzula spicata	70	1	52	13	6
Potentilla gelida	12	0	8	4	0
Primula algida	71	2	37	23	13
Veronica gentianoides	13	0	7	6	0
Total	270	9	170	66	43

proportion of seeds with a late period of germination was found in SBC and DSC soils.

SUMMARY

All investigated alpine communities have a considerable stock of viable seeds in their soils. The number of seeds ranges from several hundred for ALH to more than 10'000/m^2 for alpine bogs. The number of germinable soil seeds tends to increase from dry to moist alpine communities.
There is more correspondence between recent community composition and soil seed banks for communities developing under severe ecological conditions (ALH, DSC, MSC, BOG) than for highly productive communities (FVG, GHM, RCB). The main dominants of alpine meadows, grasslands and bushes have few or no viable seeds in permanent seed banks. (ALH = alpine lichen heaths, DSC = open communities on dry screes, MSC = open communities on moist screes, BOG = alpine bogs, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, RCB = *Rhododendron caucasicum* bush communities).
Floristic diversity (the average number of species per dm^2) is similar for recent plant communities and corresponding soil seed banks.
Most of the seeds germinated in the spring of the first year of observation. Most seeds with a late period of germination were found in SBC (snow bed communities) soils.
Two methods for studying soil seed banks are compared. The number of seedlings grown under greenhouse conditions was 1.3-8.8 times greater than those grown in the field.