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The Alpine Soil Seed Bank in Relation to Field Seedlings and Standing Vegetation in Subarctic Finland

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Abstract

This study investigated the relationship of seed bank and field seedlings on the structure of standing vegetation. We also studied the roles in sexual regeneration of seed size, diaspore morphology, and the ability to regenerate vegetatively. Seed banks, field seedlings, and standing vegetation were sampled in 8 subarctic plant communities in Kilpisjärvi, Finland, in, 1995–1998. The seed bank densities varied from 99 to, 1 109 viable seeds m^{-2-1} and decreased toward higher altitudes. The seed bank densities were significantly larger than the field seedling densities in the closed vegetation of the lower slopes, whereas the differences were smaller in the open, late-melting snowbeds on higher slopes. The species that occurred only in the seed bank had small seeds or appendaged diaspores. The field seedling densities were high in plant communities dominated by species with ineffective vegetative reproduction or by species with diaspores and with pappus. The floristic similarity was low between the seed bank, field seedlings, and standing vegetation. The nonmetric multidimensional scaling revealed that the species diversity was lower in the seed banks than in standing vegetation and field seedlings. The results indicate that all transitions equally constrain the sexual regeneration of vegetation. Clonality, very small and very large seed sizes, appendaged diaspores, and possibly narrow first leaves in seedlings are traits that limit the transition of plants from standing vegetation to the phase of field seedlings via seed bank. Persistent seed bank has a minor role compared to clonal growth in the regulation of vegetation structure.

Introduction

Clonal growth is considered the major factor in maintaining the vegetation structure in subarctic and arctic habitats. Observations on low floristic similarity between the standing vegetation and the product of sexual reproduction, the seed bank (e.g., Chambers, 1993; Kiirikki, 1993; Jensen, 1998; Holmes and Cowling, 1997; Morgan, 1998; Arroyo et al., 1999), support this finding. Although the presence of seed bank is important for recovery after disturbances, the roles of soil seed bank and the field seedlings in vegetation structure are still relatively unknown (Freedman et al., 1982; Leck and Simpson, 1995). There are four main transitions in the sexual regeneration pathway that influence the vegetation structure: seed production, accumulation of seed in the seed bank, germination of seed, and survival and growth of seedlings into adult plants. Seed production in the alpine vegetation of the subarctic region is large, at least during favourable years, but the accumulation of seed in the seed bank is generally low (Molau and Larson, 2000). Germination of seeds and survival of seedlings are constrained by several environmental factors, e.g., competition by established vegetation, seed predation, low temperatures, needle ice activity and soil drought (Chambers, 1995; Kiviniemi, 1999). High mortality of seeds and seedlings reduces the floristic similarity between the seed bank flora and seedling flora and between the seedling flora and the standing vegetation (Welling and Laine, 2000b; Leck and Simpson, 1995).

Morphological characteristics of seed, such as seed size and appendages, can influence the success of sexual regeneration and hence the floristic similarity between seed bank, field seedlings, and standing vegetation. Small seeds accumulate in the seed bank more effectively than large seeds (Thompson et al., 1998), and hence standing vegetation dominated by species with small seeds may show floristic similarity between the seed bank (Chambers, 1993). On the other hand,

the germination of small seeds and the survival of seedlings from small seeds are more vulnerable to competition, shade, nutrient deficiency and aridity compared with large seeds or seedlings (Eriksson and Jakobsson, 2000). Hence, a high proportion of small seeds in the seed bank may reduce the floristic similarity between the seed bank and the field seedlings and between field seedlings and standing vegetation. Appendaged diaspores are adapted to disperse over long distances, while their likelihood of burial in the soil may be limited (Rabinowitz, 1981). Unburied diaspores are exposed to seed predation (Hulme, 1994; Moles et al., 2000) and temporally extreme conditions, e.g., heat (Peart, 1984); hence, appendages may constrain germination and seedling recruitment. Consequently, a high proportion of plants with appendaged diaspores may limit the densities of seed banks and the field seedlings as well as the floristic similarity between the seed bank, field seedlings, and the standing vegetation.

The aim of this study was to determine the roles of the early phases in the regeneration pathway (seed bank, field seedling flora) in the determination of vegetation structure in 8 subarctic plant communities in Kilpisjärvi, northernmost Finland. We asked the following questions: (1) Are there constraints in the accumulation of seeds into persistent seed bank? (2) Are there correlations between persistent seed bank flora, field seedling flora, and standing vegetation? (3) Does the seed bank density decrease toward higher altitudes? (4) Do seed size, diaspore morphology, and the ability to reproduce vegetatively influence the success of sexual regeneration in the plant communities?

Materials and Methods

STUDY SITES AND SAMPLING

The study was carried out in the subarctic Kilpisjärvi area (69°01'N, 20°50'E), in northernmost Finland, during 1995–1998. The mean

TABLE 1
Description of plant communities

Plant community	Characterization	Altitude, m a.s.l.	Dominant species
MYRT	Heath on lower slope	600	<i>Empetrum nigrum</i> , <i>Vaccinium myrtillus</i>
CASS	Heath on upper slope	900	<i>Empetrum nigrum</i> , <i>Cassiope tetragona</i>
GRHE	Siliceous grass and sedge heath on upper slope	850	<i>Cassiope hypnoides</i> , <i>Carex bigelowii</i>
SAL	Late melting snowbed with patches of hepatics	800	<i>Cassiope hypnoides</i> , <i>Salix herbacea</i>
RANU	Late melting snowbed with patches of hepatics	845	<i>Ranunculus glacialis</i> , <i>Cassiope hypnoides</i>
EUME	Eutrophic low herb meadow	570	<i>Carex bigelowii</i> , <i>Viola biflora</i>
EUBED	Euthopic, early melting low herb snowbed	820	<i>Carex bigelowii</i> , <i>Viola biflora</i>
TALL	Tall herb meadow	560	<i>Trollius europaeus</i> , <i>Geranium sylvaticum</i>

annual precipitation of the region is 422 mm, annual temperature is -2.6°C , and the length of the growing season is 100 d (Järvinen, 1987). Treeline is formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*) at 600 m a.s.l. Eight common subarctic plant communities, at least 50 m apart, were chosen for the study (Table 1). In each plant community, 12 seed bank samples were randomly taken with a soil core (15 cm diameter \times 5 cm height) close to the transects in the first week of September 1997. At that time, most current-year seeds had not yet dispersed. Hence, we assumed most seeds to be at least 1 yr old and to represent persistent seed bank (Thompson et al., 1997). The samples were stratified and germinated twice after spreading them as a 0.5-cm-thick layer over autoclaved soil of mixed sand and gravel. The first moist stratification was done for 2 mo at 5°C in a dark, cold room (Staniforth et al., 1998), and the first germination was done in the greenhouse at 16 h of daylight (400-W lamps, 1 m apart, placed 1 m above the samples) and in 8 h of twilight (60% of the lamps switched off) for 8 mo. The twilight was used to simulate night conditions during subarctic summer. The temperatures varied diurnally from 15°C to 24°C , which ensured maximum germination during the experiment. Such temperature fluctuations facilitate the seed germination of many species (Sayers and Ward, 1966; Thompson and Grime, 1983). The second moist stratification occurred at 5°C in a dark, cold room for 4 mo, after which the second seed bank germination was carried out for 3.5 mo. The light

regimen and the daytime temperature of the second germination period were similar to the first germination period, whereas the minimum temperature was now 10°C . The samples were watered regularly during the germination periods. Seedlings were counted every second day and identified according to species.

In each plant community, 3 parallel 7-m-long transects were established 3 m apart. At each transect, 4 0.8×0.8 -m squares were placed 1.3 m apart. Field seedlings of 0–3 yr old were counted, and the cover of adult vascular plants was measured in the squares during the period from mid-July to August in 1995 and 1996. The developmental stage of field seedlings was estimated as proposed by Wager (1938) and Freedman et al. (1982). The seedlings and adult plants were identified according to species except for 5 genera: *Alchemilla* spp., *Antennaria* spp., *Cerastium* spp., *Pyrola* spp., and *Luzula* spp., the seedlings of which were classified to genus. Current-year and older seedlings were not distinguished from each other. Hence, the term “recruitment” indicates all seedlings counted in the field. Vegetation cover was estimated at 5% intervals except for the cover values under 10%, which were classified in the following categories: 0.5%, 1%, 5%, and 7%.

The species were divided into 4 regenerative groups based on their abilities to reproduce vegetatively (Söyrinki, 1938; Table 2). Diaspore morphology and seed weight classes were determined from seeds collected mostly from Kilpisjärvi during 1996–1998 (Table 2). For the determination of seed weight classes, 100 seeds per species were dried at 80°C for 3 d. Seed weights were measured after removal of the appendages.

TABLE 2

Classification into regenerative groups, diaspore morphology classes, and seed weight classes

Group/Abbreviation	Explanation
Regenerative group	
NV	No vegetative reproduction
VP	Vegetative reproduction possible, though no special organs for reproducing vegetatively
VI	Vegetative reproduction ineffective at maintaining populations
VE	Vegetative reproduction effective at maintaining populations
Diaspore morphology	
1	No apparent structures for seed dispersal and seedling recruitment
2	Diaspores with pappus
3	Diaspores with wings of fringes
4	Diaspores with fleshy fruits
5	Diaspores with awns, hooks and/or calyx
Seed weight	
1	0–0.1 mg
2	>0.1–0.5 mg
3	>0.5–1.0 mg
4	>1.0–5.0 mg
5	>5.0 mg

STATISTICS

The seed bank densities were compared between plant communities using the one-way ANOVA and the Dunn-Šidak post hoc test. Square-root transformation was used in the analyses. Within each plant community, the seed bank density was compared with the field seedling density using the t-test. Three correlations were calculated using Spearman’s rank correlation: (1) between the seed bank densities and the altitude; (2) between the seed bank densities and the relative proportions of plants of different regenerative groups, seed sizes, and morphological characters in standing vegetation; and (3) between the field seedling densities and the relative proportions of plants of different regenerative groups, seed sizes, and morphological characters in the seed banks. The SPSS 8.0 Package was used for statistical analyses.

The floristic similarity between the seed banks and the standing vegetation and between the seed banks and the field seedlings across the plant communities was tested using a nonmetric multidimensional scaling (PC-ORD Package 3.0). The empty samples were deleted before the analyses. Jaccard’s similarity coefficient was chosen as a distance coefficient. To analyze the floristic similarity between seed bank, field seedling flora, and standing vegetation, qualitative Jaccard’s

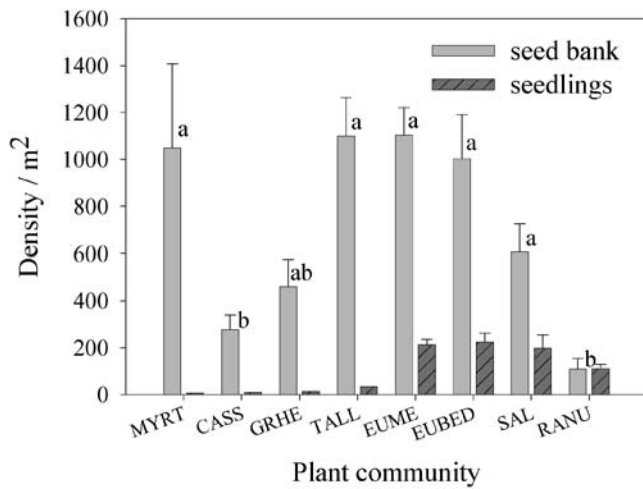


FIGURE 1. Mean seed bank densities and mean seedling densities (\pm SE) in 8 alpine plant communities. For abbreviations of plant communities, see Table 1. Different letters indicate significant differences in seed bank densities between plant communities ($P < 0.05$). Except for RANU, the difference between seed bank and field seedling densities was always significant ($P < 0.05$).

similarity coefficient (Jongman et al., 1987; Welling and Laine, 2000b) and Spearman's correlation analysis (Chambers, 1993; Booth and Larson, 1998, 2000; Welling and Laine, 2000b) were used. The equation for the qualitative Jaccard's similarity coefficient is $SJ = c/(A + B - c)$, where A = the total number of species in the seed bank, B = the total number of species in the field seedlings or in the standing vegetation, and c = the number of species shared by the seed bank and the standing vegetation or the field seedlings. Only the species occurring in both the seed bank and the field seedling flora were included in the Spearman's correlation analysis (Chambers, 1993; Booth and Larson, 2000). To examine whether the similarity between seed bank and field seedlings differed between plant communities, the one-way ANOVA and the Tamhane's post hoc test were used. The Tamhane's test is appropriate when the variances are unequal. To compare the floristic similarity between the seed bank and the standing vegetation and between the seed bank and the field seedlings, the t-test with the Dunn-Šidak correction was used. Spearman's correlation analysis was used to investigate correlations between Jaccard's similarity coefficients and the relative proportions of the plant regenerative groups in the standing vegetation and in the seed banks.

Results

THE SEED BANK AND FIELD SEEDLING DENSITIES

The seed bank density (number of seedlings emerging from the seed bank samples) ranged from 99.1 to 1108.8 seedlings m^{-2-1} (Fig. 1). The density was larger in the meadows (EUME, TALL), two snowbeds (EUBED, SAL), and the heaths of the lower slopes (MYRT) compared with RANU and the heaths of the upper slopes (CASS, GRHE). Six species, *Carex bigelowii*, *Cassiope tetragona*, *Gnaphalium supinum*, *Phyllodoce caerulea*, *Sibbaldia procumbens*, and *Veronica alpina*, formed about half, $49 \pm 11\%$, of the seed banks (Appendix 1). Most seeds of the seed bank samples germinated during the first germination period. However, several hundred seeds m^{-2-1} , mostly sedges and rushes, also germinated during the second germination period. As expected, there was a negative correlation between the seed bank densities and altitude ($R_s = -0.810$, $n = 8$, $P < 0.05$). The correlation between the seed bank densities and the relative

TABLE 3

Spearman correlation coefficients of the relative proportions of the regenerative groups, seed weight classes, and diaspore morphology with seedling densities and floristic similarities among seed bank and seedling stages. For explanations of abbreviations, see Table 2

Plant traits in the seed bank	Seedling density in the field	Floristic similarity between seed bank and phase of field seedlings
Regenerative group		
VE	*-0.714	-0.690
VI	*0.738	*0.810
VP	-0.524	-0.381
NV	0.464	0.000
Seed weight		
1	-0.238	0.000
2	0.286	-0.286
3	0.310	0.381
4	*-0.764	-0.573
Diaspore morphology		
1	-0.595	-0.262
2	*0.762	0.571
3	0.415	0.220
4	-0.596	-0.304
5	0.659	0.012

* = significant correlations at the 5% level.

proportion of the smallest seeds (weight class 1) in the standing vegetation was also negative ($R_s = -0.734$, $P < 0.05$). The main reason for this pattern was the occurrence of *Cassiope hypnoides*, a species with small seeds and no germinated seeds in the seed bank. When this species was deleted from the analysis, the correlation disappeared ($R_s = -0.048$, $n = 8$, ns). The correlations between the seed bank densities and seed weight classes and diaspore morphology classes were statistically negligible. Except for RANU, the difference between seed bank and field seedling densities was significant ($P < 0.05$, Fig. 1).

An increase in the relative proportions of species with an ability for ineffective vegetative reproduction (VI) and diaspores with pappus (diaspore morphology class 2) increased the field seedling densities (Table 3). In contrast, an increase in the relative proportions of species with an ability for effective vegetative reproduction (VE) and heavy seeds (seed weight class 4) decreased the field seedling densities (Table 3).

FLORISTIC SIMILARITY ACROSS THE PLANT COMMUNITIES

Two dimensions were appropriate to characterize the data. In the ordination of the seed bank, the first axis separated the meadows (EUME, TALL) and two snowbeds (EUBED, SAL) from the heaths (MYRT, CASS, GRHE, Fig. 2a), and the second axis separated TALL from EUME and the snowbeds. In the ordination of the field seedlings, the first axis separated the dwarf shrub heaths (CASS, MYRT) from GRHE and RANU, TALL from the low herb communities (EUME, EUBED), and the low herb communities from SAL (Fig. 2b). The second axis separated the meadows, EUBED and SAL, from the heaths and RANU. In contrast to the pattern of the seed banks, there were several distinctly separated groups in the field seedlings: the group of MYRT and CASS; the group of TALL; the group of GRHE and RANU; and the group of EUBED, EUME, and SAL. In the ordination of the standing vegetation, the first axis clearly separated the dwarf shrub heaths from the meadows, snowbeds, and GRHE (Fig. 2c). There were three distinctly separated distant groups in the ordination: the group of MYRT and CASS; the group of RANU and SAL; and the

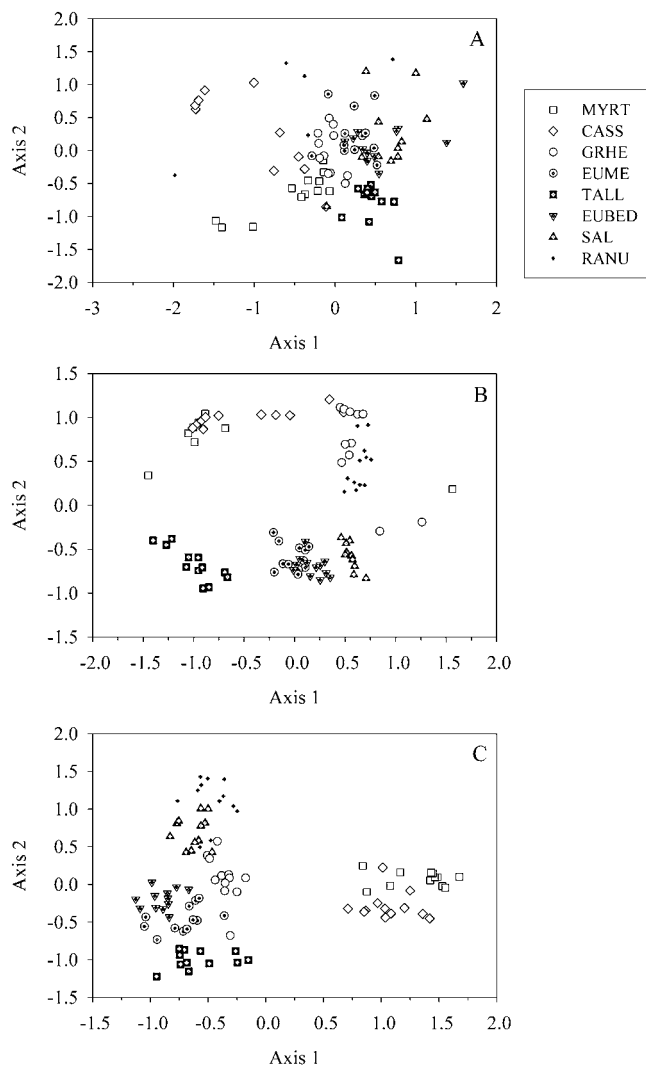


FIGURE 2. Ordinations of (a) seed banks, (b) phase of field seedlings, and (c) standing vegetation of 8 alpine plant communities in Kilpisjärvi, subarctic Finland. Nonmetric multidimensional scaling was used.

group of GRHE, EUBED, EUME, and TALL. The species richness was generally low (range from 5 to 18 species, Appendix 1).

FLORISTIC SIMILARITY WITHIN THE PLANT COMMUNITIES

The correlation between the seed bank and the field seedlings was significant only in EUBED ($R_s = 0.829$, $n = 6$, $P < 0.05$). The floristic similarity was generally low between the seed bank and the field seedlings, ranging from 0.13 to 0.39. The difference of the floristic similarities between the plant communities was statistically significant (one-way ANOVA, $F = 3.029$, $df = 7$, $P < 0.01$), but only the pairwise difference between EUBED (0.39) and TALL (0.13) was significant.

There was no correlation between the standing vegetation and the seed bank. The floristic similarity between the seed bank and the standing vegetation was generally low, ranging from 0.05 to 0.24. Despite the difference between the plant communities (one-way ANOVA, $F = 4.105$, $df = 7$, $P < 0.001$), only EUBED (0.22) differed significantly from TALL (0.09) and RANU (0.05).

There were few statistically significant differences between the Jaccard's floristic similarity coefficients between seed bank, field

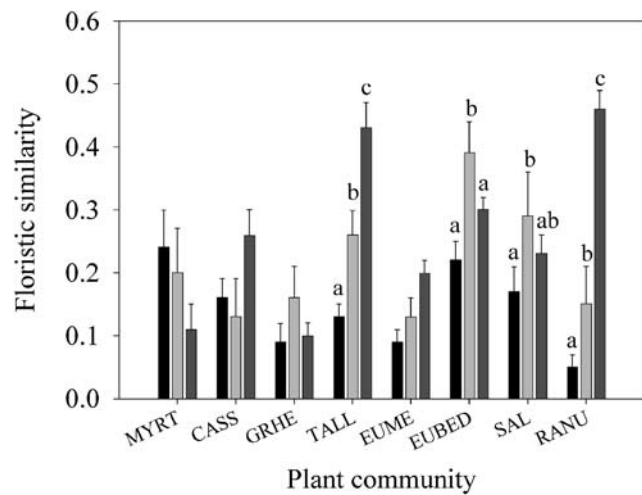


FIGURE 3. Jaccard's floristic similarities between standing vegetation and seed bank (black bars), between seed bank and field seedlings (light gray bars) and between field seedlings and standing vegetation (dark gray bars). For abbreviations of plant communities, see Table 1. $P < 0.026$. Different letters indicate significant differences between bars within each plant community.

seedling flora, and standing vegetation (Fig. 3). The similarity between the seed bank and the standing vegetation was significantly lower than that between the seed bank and the field seedlings in EUME, EUBED, SAL, and RANU. Furthermore, the standing vegetation and the field seedlings were significantly more similar than the standing vegetation and the seed bank only in EUME and RANU. There was a correlation in the floristic similarity between the seed bank and the field seedlings and the relative proportions of the plants with an ability for ineffective vegetative reproduction (VI) in the seed bank ($R_s = 0.810$, $n = 8$, $P < 0.05$, Table 3).

Most taxa that occurred only in the standing vegetation were trailing dwarf shrubs with effective vegetative reproduction (*Salix* spp., *C. hypnoides*), grasses with a low ability for vegetative reproduction and appendaged diaspores (e.g., *Poa alpina*, *Phleum alpinum*), herbs characterized by appendaged diaspores (*Antennaria* spp., *Hieracium* spp., *Petasites frigidus*, *Oxyria digyna*), and herbs characterized by heavy seeds (e.g., *Pedicularis lapponica*, *Solidago virgaurea*, *Trientalis europaea*; Table 4, Appendix 2). *Polygonum viviparum*, which reproduces primarily by bulbils, was also in this group. The taxa that were abundant in the standing vegetation were usually those with an ability for effective vegetative reproduction. Appendaged diaspores (*Betula* spp., *Taraxacum* spp., *Vaccinium* spp.) and small seeds (*Luzula* spp., *Juncus trifidus*) were common traits in the taxa that occurred only in the seed bank, and most of the taxa that occurred only among the field seedlings had appendaged diaspores (e.g., *Antennaria* spp., *Betula* spp., *Vaccinium* spp., *Saussurea alpina*). *Agrostis mertensii* is a narrow-leaved grass that could be overlooked in the cover estimations at TALL. Most taxa that occurred in the seed bank but not among the field seedlings were sedges, erect dwarf shrubs, a rush characterized by small seeds (*Juncus trifidus*), and herbs characterized by appendaged diaspores or by both large seeds and appendages (e.g., *Taraxacum* spp., *Antennaria* spp., *Ranunculus* spp., and *Oxyria digyna*). Finally, most taxa that occurred among the field seedlings but not in the seed bank were herbs characterized by large seeds (commonly above 0.5 mg) or both large seeds and appendages (e.g., *Astragalus alpinus*, *Saussurea alpina*, *Potentilla crantzii*, *Rumex acetosa*, *Solidago virgaurea*, *Trollius europaeus*) and grasses with appendages and small seeds (*Deschampsia flexuosa*, *Festuca ovina*, *Anthoxanthum odoratum*).

TABLE 4

Occurrence of taxa in the seed bank, seedling stage, and standing vegetation. For abbreviations of plant communities, see Table 1

Plant community	Taxa that occur only in standing vegetation	Taxa that occur in the seed bank but not in the phases of field seedlings or occur only in the seed bank	Taxa that occur in the phase of field seedlings but not in the seed bank or occur only in the phase of field seedlings
MYRT	<i>Cassiope hypnoides</i> <i>Juniperus communis</i> <i>Salix herbacea</i> <i>Pedicularis lapponica</i> <i>Polygonum viviparum</i> <i>Solidago virgaurea</i>	<i>Vaccinium myrtillus</i> <i>Vaccinium vitis-idaea</i> <i>Taraxacum</i> sp.* <i>Juncus trifidus</i> <i>Luzula</i> spp.*	<i>Betula</i> spp. <i>Antennaria</i> spp.
CASS	<i>Salix herbacea</i> <i>Vaccinium vitis-idaea</i> <i>Pedicularis lapponica</i> <i>Calamagrostis</i> spp.	<i>Carex</i> spp. <i>Juncus trifidus</i> *	<i>Empetrum nigrum</i> <i>Phyllodoce caerulea</i> * <i>Festuca ovina</i>
GRHE	<i>Cassiope hypnoides</i> <i>Salix herbacea</i> <i>Antennaria</i> spp. <i>Cardamine bellidifolia</i> <i>Polygonum viviparum</i> <i>Pyrola</i> spp. <i>Solidago virgaurea</i> <i>Trientalis europaea</i> <i>Anthoxanthum odoratum</i> <i>Calamagrostis lapponica</i> <i>Carex panicea</i> <i>Festuca ovina</i>	<i>Betula</i> spp.* <i>Calamagrostis</i> spp. <i>Carex bigelowii</i> <i>C. lachenalii</i>	<i>Vaccinium vitis-idaea</i> * <i>Hieracium</i> spp. <i>Minuartia biflora</i>
EUME	<i>Cassiope hypnoides</i> <i>Salix herbacea</i> <i>Campanula rotundifolia</i> <i>Cardamine bellidifolia</i> <i>Minuartia biflora</i> <i>Oxyria digyna</i> <i>Polygonum viviparum</i> <i>Rumex acetosa</i> <i>Trollius europaeus</i> <i>Festuca ovina</i> <i>Phleum alpinum</i> <i>Poa alpina</i>	<i>Betula</i> spp.* <i>Phyllodoce caerulea</i> <i>Carex lachenalii</i> <i>Juncus trifidus</i>	<i>Vaccinium myrtillus</i> * <i>Alchemilla</i> spp. <i>Antennaria</i> spp. <i>Astragalus alpinus</i> <i>Cerastium</i> spp. <i>Hieracium</i> spp. <i>Potentilla crantzii</i> <i>Ranunculus</i> spp. <i>Saussurea alpina</i> <i>Solidago virgaurea</i> <i>Deschampsia flexuosa</i> <i>Festuca ovina</i>
TALL	<i>Empetrum nigrum</i> <i>Linnea borealis</i> <i>Rubus saxatilis</i> <i>Vaccinium vitis-idaea</i> <i>Achillea millefolium</i> <i>Bartsia alpina</i> <i>Hieracium sylvatica</i> <i>Hieracium nigrescentia</i> <i>Minuartia biflora</i> <i>Myosotis</i> sp. <i>Petasites frigidus</i> <i>Polygonum viviparum</i> <i>Pyrola</i> spp. <i>Solidago virgaurea</i> <i>Taraxacum</i> spp. <i>Thalictrum alpinum</i> <i>Veronica alpina</i> <i>Calamagrostis</i> spp. <i>Festuca ovina</i> <i>Luzula</i> spp. <i>Phleum alpinum</i> <i>Trisetum spicatum</i>	<i>Phyllodoce caerulea</i> * <i>Vaccinium myrtillus</i> * <i>Antennaria</i> spp. <i>Hieracium</i> spp. <i>Ranunculus</i> spp. <i>Sibbaldia procumbens</i> <i>Agrostis mertensii</i> (*) <i>Carex bigelowii</i> <i>Deschampsia flexuosa</i> <i>Festuca rubra</i> *	<i>Rumex acetosa</i> <i>Saussurea alpina</i> <i>Trollius europaeus</i>
EUBED	<i>Salix herbacea</i> <i>S. polaris</i> <i>Antennaria</i> spp. <i>Cassiope hypnoides</i> <i>Hieracium alpina</i>	<i>Vaccinium myrtillus</i> <i>Oxyria digyna</i> * <i>Carex bigelowii</i> <i>C. lachenalii</i> <i>Juncus trifidus</i>	<i>Cardamine bellidifolia</i> * <i>Cerastium</i> spp. <i>Saussurea alpina</i>

TABLE 4
(Cont.)

Plant community	Taxa that occur only in standing vegetation	Taxa that occur in the seed bank but not in the phases of field seedlings or occur only in the seed bank	Taxa that occur in the phase of field seedlings but not in the seed bank or occur only in the phase of field seedlings
	<i>Polygonum viviparum</i> <i>Pyrola</i> spp. <i>Rhodiola rosea</i> <i>Solidago virgaurea</i> <i>Thalictrum alpinum</i> <i>Calamagrostis</i> sp. <i>Festuca ovina</i> <i>Poa alpina</i>		
SAL	<i>Betula nana</i> <i>Cassiope hypnoides</i> <i>Phyllodoce caerulea</i> <i>Salix herbacea</i> <i>Deschampsia flexuosa</i>	<i>Betula</i> spp. <i>Antennaria</i> spp.	<i>Hieracium</i> spp. <i>Solidago virgaurea</i> * <i>Anthoxanthum odoratum</i> <i>Luzula</i> spp. <i>Trisetum spicatum</i> *
RANU	<i>Cassiope hypnoides</i> <i>Cassiope tetragona</i> <i>Empetrum nigrum</i> <i>Phyllodoce caerulea</i> <i>Salix polaris</i> <i>Veronica alpina</i> <i>Deschampsia flexuosa</i>	<i>Salix herbacea</i> <i>Juncus trifidus</i>	<i>Ranunculus pygmaeus</i> <i>Sibbaldia procumbens</i> <i>Taraxacum</i> spp.* <i>Carex lachenalii</i> <i>Festuca ovina</i> <i>Trisetum spicatum</i> <i>Vahlodea atropurpurea</i>

* = taxa that occur only in the seed banks or in the phase of field seedlings.

Discussion

SEED BANK DENSITIES

Before this investigation, very low seed bank densities were found in the alpine area of the Fennoscandian subarctic region (Diemer and Prock, 1993; Molau and Larson, 2000). The seed bank densities in Kilpisjärvi are more like those in alpine areas of more southern regions (Hatt, 1991; Diemer and Prock, 1993; Chambers, 1993), subarctic forests of northern Finland (Vieno et al., 1993) or arctic regions (e.g., Fox, 1983; Leck, 1980; Freedman et al., 1982; Roach, 1983). Although not investigated in our study, one reason for the surprisingly high densities in Kilpisjärvi may be intensive grazing by reindeer and rodents. Grazing facilitates the colonization of low-statured herbs and graminoids (Virtanen et al., 1997), which formed the majority of the seed banks, e.g., *Veronica alpina*, *Sibbaldia procumbens*, *Gnaphalium supinum*, and *Luzula* spp. These species are mostly absent in the seed banks of northern Sweden (Molau and Larson, 2000). Our observations supported earlier findings of decreasing seed bank densities toward higher altitudes (Thompson, 1978; Molau and Larson, 2000). The reason may be in the decreasing seed production and seed quality in the higher altitudes (Laine et al., 1995). On the other hand, the denser vegetation on the lower slopes limits seedling recruitment and seemed to negate the influence of the altitude on the field seedlings (see also Welling and Laine, 2000a).

Plant traits, i.e., the dominant seed size and diaspore morphology and the ability of vegetation to produce vegetatively, should have an influence on seed bank densities (Freedman et al., 1982; Chambers, 1993). However, the relationships were not clear in this study, probably because none of these traits clearly dominated in standing vegetation. Small- and intermediate-seeded taxa can be relicts from the period when they occurred in the standing vegetation. *Luzula* spp. and *C. bigelowii* have a seed bank that may persist over 200 yr in the soil (McGraw et al., 1991; Thompson et al., 1997). However, small seed size alone does not guarantee accumulation in the seed bank if the seeds are physiologically short-lived, as in *C. tetragona* and *Vaccinium* spp.

(Thompson et al., 1997) or *Salix* spp. (Beerling, 1998). Also, larger seeds may sometimes live longer than smaller seeds in the seed bank, as in certain *Carex* spp., where species with large seeds remain dormant, while germination percentage is significantly higher for smaller seeds (Schütz and Rave, 1999; Schütz, 2000). Considering diaspore morphology, appendages are assumed to facilitate dispersal but have a negative influence on the seed bank accumulation ability (Rabinowitz, 1981). For example, in *Gnaphalium supinum*, which has diaspores with pappus, the positive influence of small seed size on seed burial seemed to overwhelm the negative influence of pappus. The appendaged diaspores of this species were common in the seed bank, although the species was uncommon in standing vegetation. On the other hand, the high number of diaspores of *Gnaphalium supinum* may have partially been an outcome of long-distance dispersal.

FLORISTIC SIMILARITY ACROSS THE PLANT COMMUNITIES

According to nonmetric multidimensional scaling, the seed banks were not as clearly separated into plant communities as the field seedlings and the standing vegetation. One reason was the low species richness of the seed banks. Morgan (1998) and Holmes and Cowling (1997) found the same phenomenon in grasslands and fynbos shrublands. In this study, the poverty and similarity of the seed banks between plant communities may be based on the temporally dynamic nature of seed banks (Simpson et al., 1989) and the importance of *Carex* spp. in all seed banks. At the time of sampling, the seed banks were probably at their most depleted state since most current-year seeds had not yet dispersed and many previous-year seeds had germinated in the field or lost their viability. This is why the species richness in the seed banks was considerably lower than in the standing vegetation. *Carex bigelowii*, a common species of almost all plant communities, forms a persistent seed bank (McGraw et al., 1991; Thompson et al., 1997), which facilitates the accumulation of large seed banks also in the communities where the coverage of *C. bigelowii* is low.

A majority of the species that occurred in standing vegetation were not found in the seed bank or among the field seedlings. Seeds of these species may have been consumed by herbivores or otherwise destroyed. Also, the small size of the first leaves may have limited the seedling recruitment of graminoids. Large seeds have a contrasting performance at seed bank, field seedling, and standing vegetation stages. Large seeds accumulate poorly in the seed bank due in part to seed predation (Thompson et al., 1998; Eriksson and Jakobsson, 2000), but their abundant nutrient resources increase their germination rate and seedling survival, especially in a stressed environment (Kiviniemi, 1999; Eriksson and Jakobsson, 2000). Despite a relatively high density of large seeds in the seed bank in this study, seedling recruitment was low. A thick moss cover may have reduced the germination of large seeds in the heaths where they were common.

Many clonal plants accumulate a seed bank, but seedling recruitment is rare (Eriksson, 1992). This is probably why there was a negative correlation between the relative proportion of plants with an ability for effective vegetative reproduction in the seed banks and the field seedling densities. On the other hand, species characterized by an ineffective vegetative reproduction ability were effective in both seed bank accumulation and seedling recruitment. Li et al. (1999) demonstrated the deviation in these abilities within the *Rhus* genus. Both weakly clonal and strongly clonal species have persistent and large seed banks. However, seedling recruitment is effective in the former, but not in the latter species.

Grazing may also have reduced the floristic similarity between the seed bank and the standing vegetation, since the low-statured species that benefit from grazing (Virtanen et al., 1997) were abundant in the seed banks but had a low coverage in the standing vegetation.

The changes in the floristic similarity from seed bank to field seedlings and from field seedlings to standing vegetation were usually equally critical. There was a significant correlation between the seed bank and the field seedlings only in EUBED. Thus, there are restrictions at every studied phase along the regeneration pathway. Eutrophic and moist conditions provide suitable conditions for field seedlings in EUBED. In this community, seed number (seed availability) determines the structure of the field seedlings; studies in the Patagonian steppe have led to similar findings (Aguiar and Sala, 1997). In TALL, tall and closed standing vegetation resulted in the poor regeneration via the field seedling recruitment and therefore the low floristic similarity between the standing vegetation and the seed bank. In RANU, the transient seed bank of *Ranunculus glacialis* (Thompson et al., 1997) and very low species richness are probably the main factors that resulted in the low floristic similarity between the standing vegetation and the seed bank. These factors were reasons for the clearly lower floristic similarity between the standing vegetation and the seed bank in TALL and RANU than in EUBED, as well as for the clearly lower floristic similarity between the seed bank and the field seedlings of TALL than in EUBED.

Conclusions

The densities of the persistent seed banks were large in the alpine vegetation of northernmost Finland. However, the floristic similarity between the seed bank, field seedlings, and standing vegetation was low, indicating that a persistent seed bank has little impact on the vegetation structure. Hence vegetative growth may have a crucial role in the maintenance of vegetation structure in these plant communities. However, the seed rain of the previous year (the transient seed bank), which was not investigated in this study, may also partially regulate the vegetation structure. This is supported by three findings: (1) many species that occurred in standing vegetation but not in the seed bank

had large seeds and poor vegetative reproduction. Since large seeds accumulate poorly in the seed bank, they have apparently germinated soon after dispersal. (2) Many species that occurred in the phase of field seedlings and in standing vegetation were not found in the seed bank. (3) The seed bank was poorer in species diversity than the field seedlings. The latter findings also lead to an assumption that germination has happened quickly after seed dispersal.

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APPENDIX 1

The mean densities of species / m² in the seed banks of 8 plant communities. For abbreviations of plant communities, see Table 1. N = 12

Taxa	Plant community type							
	MYRT	CASS	GRHE	RANU	SAL	EUBED	EUME	TALL
Dwarf shrubs								
<i>Betula</i> sp.	3.7		28.3		23.6	23.6	33.0	122.7
<i>Cassiope tetragona</i>		169.9						
<i>Empetrum nigrum</i>	113.2	28.3						
<i>Phyllodoce caerulea</i>	608.6						4.7	14.2
<i>Salix herbacea</i>				9.4				
<i>Vaccinium myrtillus</i>	9.4							9.4
<i>Vaccinium vitis-idaea</i>	4.7					4.7		
Herbs								
<i>Alchemilla</i> sp.								14.2
<i>Antennaria</i> sp.					14.2			4.7
<i>Campanula rotundifolia</i>								386.9
<i>Cardamine bellidifolia</i>				9.4				
<i>Cerastium</i> sp.								141.5
<i>Euphrasia frigida</i>							4.7	
<i>Gnaphalium supinum</i>			9.4	4.7	448.2	108.5	33.0	
<i>Hieracium Alpina</i>								9.4
<i>Oxyria digyna</i>				9.4		4.7		
<i>Potentilla crantzii</i>								94.4
<i>Ranunculus</i> sp.								4.7
<i>Ranunculus glacialis</i>				4.7				
<i>Sibbaldia procumbens</i>			33.0		28.3	151.0	302.0	4.7
<i>Taraxacum</i> sp.	4.7					23.6	4.7	
<i>Veronica alpina</i>						396.3	61.3	
<i>Viola biflora</i>						33.0	9.4	4.7
Graminoids								
<i>Agrostis mertensii</i>					23.6	18.9	146.3	127.4
<i>Anthoxanthum odoratum</i>						9.4	99.1	9.4
<i>Calamagrostis</i> sp.			9.4					
<i>Carex</i> sp.	4.7	33.1	18.9	23.6	4.7	37.7	18.9	4.7
<i>Carex bigelowii</i>	226.5	9.4	99.1		14.2	84.9	146.3	18.9
<i>Carex lachenalii</i>			23.6		18.9	56.6	28.3	
<i>Deschampsia flexuosa</i>								47.2
<i>Festuca rubra</i>								4.7
<i>Juncus trifidus</i>	28.3	9.4	61.3	14.2	33.1	28.3	23.6	
<i>Luzula</i> sp.	4.7	14.2	151.0	33.1		18.9	165.1	37.7
<i>Graminea</i>	4.7		4.7			4.7	28.3	33.0
<i>Poacea</i>								4.7
<i>Cyperaceae</i>		14.2	4.7					
Unknown graminoids	4.7		18.9			4.7		4.7
Species richness	9	5	8	8	8	14	14	18

Plant traits in the standing vegetation. 1 = regenerative group; 2 = abundance of seedling phase; Sw = seed weight; Dm = diaspore morphology; SA = seedlings are abundant; SR = seedlings are rare; NS = no seedlings (according to Söyrinki, 1938); NV = no vegetative reproduction; VP = vegetative reproduction possible, though the species has no special organs for vegetative reproduction; VI = vegetative reproduction ineffective at maintaining populations; and VE = vegetative reproduction effective at maintaining populations. Seed weight classes: 1 = 0–0.1 mg, 2 = >0.1–0.5 mg, 3 = >0.5–1.0 mg, 4 = >1.0–5.0 mg, 5 = >5.0 mg. Diaspore morphology: 1 = no apparent structure for seed dispersal or seedling recruitment, 2 = diaspores with pappus, 3 = diaspores with wings or fringes, 4 = fleshy fruits, and 5 = diaspores with awns, hooks, and/or calyx

TAXA	1	2	Sw	Dm
Dwarf shrubs				
<i>Betula nana</i>	SA	VE	2	3
<i>Cassiope hypnoides</i>	SR	VE	1	1
<i>Cassiope tetragona</i>	SA	VP	1	1
<i>Empetrum nigrum</i>	SA	VE	4	4
<i>Juniperus communis</i>	SR	VP	5	4
<i>Linnea borealis</i>	NS	VE	4	5
<i>Phyllodoce caerulea</i>	SA	VP	1	1
<i>Rubus saxatilis</i>	NS	VE	4	4
<i>Salix glauca</i>	SA	VP	1	2
<i>Salix herbacea</i>	SR	VE	1	2
<i>Salix polaris</i>	NS	VE	1	2
<i>Vaccinium myrtillus</i>	SR	VE	2	4
<i>Vaccinium vitis-idaea</i>	SR	VE	2	4
Herbs				
<i>Achillea millefolium</i>		VE	2	2
<i>Alchemilla</i> sp.	SA	NV	2	5
<i>Antennaria</i> sp.	SR	VE	1	2
<i>Antennaria alpina</i>	SR	VE	1	2
<i>Antennaria dioica</i>	SR	VE	1	2
<i>Astragalus alpinus</i>	SA	VI	4	1
<i>Bartsia alpina</i>	SA	VE	2	3
<i>Campanula rotundifolia</i>	SR	VE	1	1
<i>Cardamine bellidifolia</i>	SA	NV	2	1
<i>Cerastium</i> sp.	SA	VP		1
<i>Cerastium alpinum</i>	SA	VP	2	1
<i>Cerastium arcticum</i>	SA	VP		1
<i>Cerastium cerastoides</i>	SA	VP	1	1
<i>Cerastium fontanum</i>	SA	VP		1
<i>Geranium sylvaticum</i>	SA	NV	4	1
<i>Gnaphalium supinum</i>	SA	VI	1	2
<i>Hieracium</i> sp.	SA	NV		2
<i>Hieracium alpina</i>	SA	NV	3	2
<i>Hieracium Nigrescentia</i>	SA	NV		2
<i>Hieracium Sylvatica</i>	SA	NV	2	2
<i>Hieracium Vulgata</i>	SA	NV		2
<i>Minuartia biflora</i>	SA	NV		1
<i>Myosotis</i> sp.		VP		1
<i>Oxyria digyna</i>	SA	VP	3	3
<i>Pedicularis lapponica</i>	SR	VE	3	1
<i>Petasites frigidus</i>	NS	VE		2
<i>Polygonum viviparum</i>	SR	VE		
<i>Potentilla crantzii</i>	SA	VP	3	1
<i>Pyrola</i> sp.	SR	VE	1	1
<i>Pyrola minor</i>	SR	VE	1	1
<i>Ranunculus acris</i>	SA	VP	4	5
<i>Ranunculus auricomus</i>	SA	AP		5
<i>Ranunculus glacialis</i>	SA	NV	2	5
<i>Ranunculus nivalis</i>	SA	NV	2	5
<i>Ranunculus pygmaeus</i>	SA	NV	1	5
<i>Rhodiola rosea</i>	SA	VP	2	1
<i>Rumex acetosa</i>		NV	3	3

(Cont.).

TAXA	1	2	Sw	Dm
<i>Saussurea alpina</i>	SR	VE	4	2
<i>Sibbaldia procumbens</i>	SA	VP	3	1
<i>Solidago virgaurea</i>	SA	VP	3	2
<i>Taraxacum</i> sp.	SA	NV	3	2
<i>Thalictrum alpinum</i>	SA	VE	2	1
<i>Trientalis europaea</i>	SR	VE	3	1
<i>Trollius europaeus</i>	SA	NV	3	1
<i>Veronica alpina</i>	SA	VI	1	1
<i>Viola biflora</i>	SA	NV	3	1
Grasses and sedges				
<i>Agrostis mertensii</i>	SA	VP	1	5
<i>Anthoxanthum odoratum</i>	SA	VI	2	5
<i>Calamagrostis</i> sp.			2	5
<i>Calamagrostis lapponica</i>	SR	VE	2	5
<i>Calamagrostis purpurea</i>	NS	VE		5
<i>Carex</i> sp.				1
<i>Carex bigelowii</i>	SA	VE	3	1
<i>Carex lachenalii</i>	SA	VP	2	1
<i>Carex panicea</i>		VE	3	1
<i>Carex vaginata</i>	SR	VE	4	1
<i>Deschampsia flexuosa</i>	SA	VE	2	5
<i>Festuca ovina</i>	SA	VP	2	5
<i>Juncus trifidus</i>	SA	VI	1	1
<i>Luzula</i> sp.			2	1
<i>Luzula arcuata</i>	SA	VI	2	1
<i>Luzula multiflora</i>	SA	VP	2	1
<i>Luzula spicata</i>	SA	VP	2	1
<i>Phleum alpinum</i>	SA	VP	2	5
<i>Poa alpina</i>	SA	NV	2	5
<i>Trisetum spicatum</i>	SA	VP	2	5
<i>Vahlodea atropurpurea</i>	SA	VP	2	5