

**REGENERATION BY SEEDS  
AND VEGETATION  
STRUCTURE IN ALPINE  
PLANT COMMUNITIES,  
SUBARCTIC FINLAND**

**PIRJO  
WELLING**

Department of Biology,  
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*PIRJO WELLING*

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## *Abstract*

The aims were to examine the importance of regeneration by seeds, the influence of plant traits and disturbances, and the role of seed-seedling conflicts in regeneration and in the determination of vegetation structure. The study was carried out at in a subarctic alpine area (Kilpisjärvi 69°01'N 20°50'E, Finland).

Seed bank and seedling densities were high in many plant communities (ranges 99 -1109 viable seeds/m<sup>2</sup> and 0.2-227 seedlings/m<sup>2</sup>, respectively). Effective seedling recruitment is reflected in vegetation as a high proportion of plants with poor or no vegetative reproduction ability. This development may take place in meadows and snowbeds where herbs (e.g. *Gnaphalium supinum*, *Sibbaldia procumbens*, *Veronica alpina* and *Viola biflora*) are abundant. On the other hand, the low proportion of these plants in heath vegetation reflects ineffective seedling recruitment.

Floristic similarities between the consecutive phases in the regeneration pathway may be low despite effective seedling recruitment. Clonality, large and small seed sizes and appendaged diaspores limit the movement of species from phase to phase.

Generally, disturbances facilitate effective regeneration by seeds. Grazing promotes species with large seed banks and is therefore one reason for high seed bank densities. Freezing and melting processes negate a negative influence of altitude on seed bank densities in the phase of seedlings. However, if disturbances are severe and continuous and the soil is compact, unstable or dry, disturbances are not beneficial. The same is true if there is a shift in the species composition of seedlings from gaps to closed vegetation. This phenomenon occurred in a rich meadow.

Seed-seedling conflicts limit regeneration by seeds in low-herb snowbeds and *Ranunculus glacialis*-*Gymnomitrium* snowbeds. Vegetative reproduction and infrequent pulses of seedling recruitment negate an influence of short-term seedling recruitment on the spatial structure of vegetation. Extreme conditions, such as low temperatures, instability of the soil and late snowmelt modify the influence of factors that are important in more moderate conditions.

To conclude, all transitions limit regeneration by seeds. However, favourable conditions (e.g. moist conditions in a meadow) partly eliminate the obstacles against seedling emergence. Regeneration by seeds therefore has a major impact on the dynamics and structure of vegetation. In heath vegetation, where bare soils are dry and the moss cover is thick, large seed banks and seed rains do not guarantee effective seedling recruitment. The regeneration process is reduced in the early phases, and plants that reproduce primarily by seeds have a minor role in vegetation. The accumulation of seed banks is effective in these circumstances.

*Keywords:* seed bank, seed rain, seedling emergence, seedling recruitment



*To my mother*

**“Before practising, rivers were rivers and mountains were mountains. When I practised, I saw the rivers were no longer rivers and mountains were no longer mountains. Now I see that rivers are again rivers and mountains are mountains.”**

A Zen-master

**“...all that is produced in dependence (of causes and conditions) has neither death nor birth, annihilation nor permanence, No going nor coming, sameness nor difference, It is free of conceptions and is at peace.”**

Nagarjuna



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Oulu, 8<sup>th</sup> October 2002

Pirjo Welling



## Definitions

phase	stages during regeneration, e.g. seed rain, seedling emergence, standing vegetation
regeneration pathway	the process of regeneration from seed production to standing vegetation
seedling emergence	the density of seedlings that have grown above the soil
seedling flora	field seedlings
seedling recruitment	the density of seedlings that have survived for at least two years
vegetation structure	the spatial arrangement and relative relationships of plants within a plant community



## List of original papers

This thesis is based on the following papers which are referred to in the text by their Roman numerals:

- I Welling P & Laine K (2000) Characteristics of the seedling flora in alpine vegetation, subarctic Finland I. Seedling densities in 15 plant communities. *Ann Bot Fenn* 37: 69-76.
- II Welling P & Laine K (2000) Characteristics of the seedling flora in alpine vegetation, subarctic Finland II. Floristic similarity between seedling flora and mature vegetation. *Ann Bot Fenn* 37: 133-137.
- III Welling P & Laine K (2002) The alpine soil seed bank relationship to field seedlings and standing vegetation in subarctic Finland. Submitted.
- IV Welling P & Laine K (2002) Regeneration by seeds in alpine meadow and heath vegetation in subarctic Finland. *J Veg Sci* 13: 217-226.
- V Welling P & Laine K (2002) Quantitative plant trait spectra in the regeneration of two alpine plant communities in subarctic Finland. Manuscript.
- VI Welling P & Laine K (2002) Influence of micro-spatial heterogeneity on regeneration in two mid-alpine snow bed communities. Manuscript.



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# 1 Introduction

## 1.1 Regeneration by seeds in northern and alpine areas

Until recently, many researchers have assumed that regeneration by seeds has little significance in the development and maintenance of subarctic, arctic and alpine plant communities (Bliss 1971, Billings 1974, Johnson 1975, Archibold 1984, 1995). Regeneration should take place mainly by vegetative means in these harsh areas. Seed production often fails, and seedling survival is low (Wager 1938, Billings 1974). Furthermore, it has been assumed that, in mountainous areas, regeneration by seeds is more risky on the higher than the lower slopes (Maruta 1983, 1994, Montalvo *et al.* 1991). These assumptions are still often accepted, despite several reports to the contrary, *e.g.* Söyrinki 1938, Freedman *et al.* 1982, McGraw & Shaver 1982, Chambers 1993, Urbanska & Fattorini 2000.

Information about seed banks in the Subarctic is still scarce and therefore highly contradictory. No seeds germinated in samples collected from a lichen woodland (Johnson 1975), a wet sedge-grass community, a dry ericaceous heath and a treeline stand in Canada (Archibold 1984). However, Vieno *et al.* (1993) and Komulainen *et al.* (1994) found 579-1239 viable seeds /m<sup>2</sup> and 225-416 viable seeds / m<sup>2</sup> in seed banks of pine-birch and pine forests in Finnish Lapland and on the Kola Peninsula, respectively. The total density of a seed bank in a salt marsh in subarctic Canada was larger than in marshes of temperate areas, *i.e.* 39 204 viable seeds / m<sup>2</sup> (Staniford *et al.* 1998).

As far as I know, only one investigation has analysed seedling densities in alpine areas in the Subarctic, namely the work by Söyrinki (1938). The present work demonstrated very high seedling densities in many plant communities. This suggests large seed rains and seed banks. Indeed, Molau and Larson (2000) reported several hundreds of seeds in the seed rain in Subarctic Sweden. Unexpectedly, very low seed bank densities (range of means 0-37 viable seeds/ m<sup>2</sup>) have been reported (Diemer & Prock 1993, Molau & Larson 2000).

## 1.2 Regeneration by seeds in plant communities

### *1.2.1 Relationships of standing vegetation to seed rain, seed bank and seedlings*

Seed rain includes all individuals (seeds) that arrive at a site (Fig. 1a, Booth & Larson 1998). Seed rain includes seeds from local, adjacent and distant plant communities. Many species that occur in adjacent or distant plant communities may contribute to the seed rain of a plant community where these species cannot be recruited into the standing vegetation (Schott & Hamburg 1997, Booth & Larson 1998). The information concerning floristic similarity between the standing vegetation and the seed rain is contradictory (Chambers 1993, Booth & Larson 1998, Jensen 1998). A limited ability of seeds to disperse in space increases this similarity. However, if the species that produce a persistent seed bank and have a pulsed mode of seed production are abundant in the standing vegetation, this similarity is low (Rabinowitz 1981). Since the seed rain follows immediately the phase of standing vegetation, and fewer obstacles have challenged the plants than in the later phases, there is reason to expect that the standing vegetation and the seed rain are more similar to each other than the standing vegetation and the other phases. Thus, the structure of the seed rain could possibly be predicted more reliably from the structure of the standing vegetation than from the structure of the later phases.

While studies on the relationships between the standing vegetation and the seed rain are still scarce, the literature concerning the mutual relations of the standing vegetation and the seed bank is extensive (Fig. 1a, *e.g.* Leck *et al.* 1989, Hyatt & Casper 2000, Funes *et al.* 2001). In temperate regions, floristic similarity often decreases during the succession of vegetation (Kiirikki 1993, Jensen 1998). The reason for this is that the species from the pioneer and early successional stages are not present in the standing vegetation of the late successional stages but are common in the seed banks of these later stages. In alpine and arctic areas, species and life history pools are poorer than in temperate areas (Chambers 1995). For instance, annuals and biennials, which are common in temperate plant communities, are rare in alpine and arctic communities. This results in less distinct successional stages and more overlap in the floristic compositions between the seed bank and the standing vegetation compared to temperate areas (Chambers 1993). However, Freedman *et al.* (1982) did not find statistically significant correlations between the standing vegetation and the seed bank within the plant communities of Ellesmere Island, High Arctic Canada. Ruderal-like species with an ability to produce larger numbers of viable seeds were dominant in the seed banks. On the other hand, stress tolerators were dominant in the standing vegetation. Furthermore, in the central Chilean Andes, downslope dispersal and runoff led to relatively low similarity between the seed bank and the standing vegetation (Arroyo *et al.* 1999). Chambers (1993) demonstrated that the standing vegetation and the seed bank are more similar to each other in severely disturbed than in relatively undisturbed vegetation.

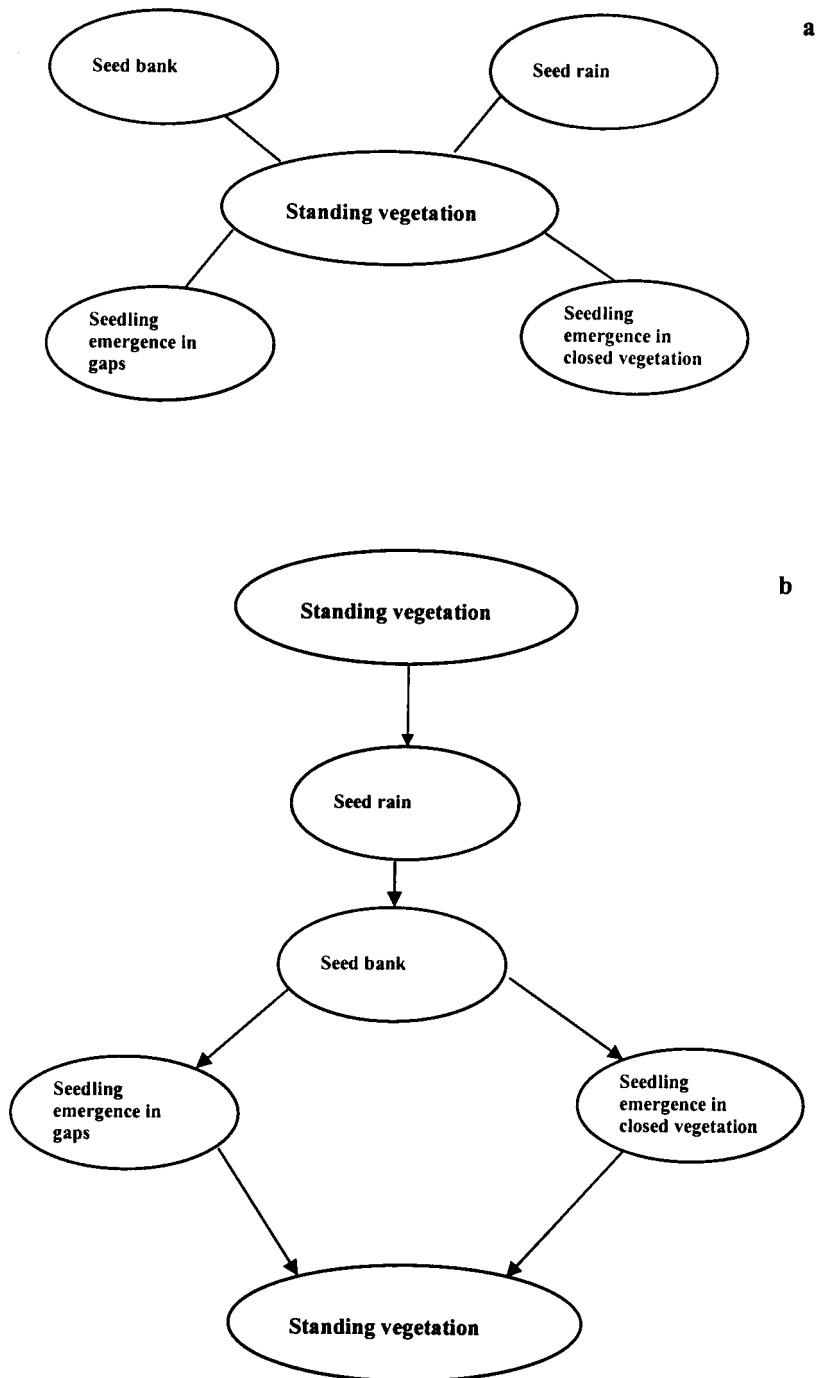


Fig. 1. Relationships between the standing vegetation and the other phases in the regeneration pathway (a) and the regeneration pathway (b).

There is little information about the relationships between the standing vegetation and seedlings (Fig. 1a). This is a major deficiency because the structure of the phase of seedlings may reflect the actual significance of regeneration by seeds in the development and maintenance of plant communities more accurately than the earlier phases. Freedman *et al.* (1982) found significant correlations between the standing vegetation and seedlings in only half of the communities studied at Ellesmere Island, Canada. The coverage of dominant perennials was not related to the seed bank densities of these perennials in a tidal freshwater marsh (Leck & Simpson 1995).

### ***1.2.2 Process of regeneration in patchy environments***

Most investigations have focused on a single phase of regeneration (usually the seed bank) in addition to the standing vegetation. Many studies have also documented the regeneration processes of a limited number of species in a plant community (Aguiar *et al.* 1992, Aguiar & Sala 1994 & 1997). These approaches have left space for an effort to understand the process of regeneration as a whole from the perspective of the plant community and the role of these processes in determining the vegetation structure.

Seed rain is an early phase in the process of regeneration (Fig. 1b). Features of the microenvironment after the seeds have landed on the ground influence the movement of individuals to the following phases. Seeds may germinate rapidly after they have landed, be incorporated into the viable seed bank or die after or before burial (Simpson *et al.* 1989). Seeds that are not buried or are buried near the soil surface are more short-lived than seeds that are buried in the deeper layers. This is because seeds on the ground are exposed to temporally fluctuating factors, *e.g.* melting and freezing processes and temperature variation (Chambers 1993). Seeds that are not buried are also exposed to seed predation (Hulme 1998, Auld & Tenham 1999, Hubbard & McPherson 2000). Pathogens and ageing destroy the viable seed bank in soil. Drought and low temperatures reduce the germination of seeds. Needle ice activity, soil drought, grazing and slow seedling growth influence seedling survival and limit seedling recruitment (Chambers 1995). Seedling growth and survival is better in long, warm growing seasons than in short, cool growing seasons. The addition of nutrients may increase or decrease the survival of plants. Thus, many factors challenge plants during their development, and the obstacles vary from phase to phase. These challenges have consequences for the process of regeneration and the features of the vegetation structure.

The high proportion of species characterised by persistent seeds in the seed banks and the high proportion of species characterised by transient seeds in the seed rain reduce the floristic similarity between the seed bank and the seed rain (Fig. 1b, Schott & Hamburg 1997, Booth & Larson 2000). A low level of similarity has been documented between the seed bank and seedlings (Freedman *et al.* 1982, Piroznikow 1983, Leck & Simpson 1995). Edwards and Crawley (1999) demonstrated recently that, in a grassland characterised by a large seed bank, few seedlings and only two species were recruited into the seedlings from the seed bank.

Marked micro-scale heterogeneity in the distribution of seeds and seedlings is a common feature (Peart 1989, Rusch 1992, Rusch & Fernandez-Palacios 1995, Schupp & Fuentes 1995). Because of the limited dispersal distance of seeds, the density of seed rain

declines leptokurtically with distance: the majority of seeds drop in the vicinity of their parents and the tail of long distance dispersal is extended (Nathan & Muller-Landau 2000). After the primary seed dispersal, a secondary seed dispersal (horizontal and vertical movement after the first landing) and seed predation influence the distribution of seeds. The temporal and spatial variation of this distribution is poorly known. The micro-scale variation in the abundance of seeds trapped by soil is a primary factor that determines the spatial distribution of seed germination. The micro-sites that are suitable for the arrival of seeds are not, however, necessarily suitable for seed germination. Further, the micro-sites that are suitable for seed germination are not necessarily suitable for seedling survival, those suitable for seedling survival may not be suitable for the growth and survival of juveniles, and finally, the micro-sites that promote the growth and survival of juveniles may not always be suitable for the growth and survival of adults (Schupp & Fuentes 1995). These seed-seedling conflicts may result in shifts in the micro-scale distributions of different development phases and limit the actual seed regeneration ability of populations. This knowledge raises the question of whether these conflicts influence the spatial structure of vegetation. And if they do, which process is critical and determines this structure.

### ***1.2.3 Influence of plant traits on regeneration by seeds***

Functional groups provide one of the many approaches to observe and analyse vegetation structure. Research on the predictability of changes in plant communities across a wide range of areas and processes has emphasised the usefulness of the subdivision of species into a small number of functional groups (*e.g.* Pillar 1999, McIntyre *et al.* 1999, Lavorel *et al.* 1999). Functional groups include several traits of potential functional significance (Semenova & van der Maarel 2000). There is much variation in the composition of trait lists across investigations (*e.g.* Leishman & Westoby 1992, Díaz *et al.* 1999, Allesor *et al.* 1999, Weiher *et al.* 1999). This variation is due to the characteristics of vegetation and the process or pattern that is of interest. Mabry *et al.* (2000) subdivided traits into three groups. Reproductive traits include the characteristics of seeds, dispersal, pollination and flowers. Vegetative traits include growth forms, types of clonal spreading and leaf types. Phenological traits include the timing of flowering, dispersal and leafing. Reproductive traits influence directly the regeneration of populations, and the proportions of these traits in a plant community should influence directly the process of regeneration of plant communities. There is also evidence to suggest that clonality has consequences for regeneration (Eriksson 1997). In addition, generalisations about the pattern of regeneration by seeds have been made from growth forms (Grime *et al.* 1981, Chambers *et al.* 1987, Schütz & Rave 1999).

Small seeds tend to be more abundant in persistent seed banks than large ones (Thompson *et al.* 1998), which increases the proportion of small seeds in seed pools. Seed size also influences seedling emergence in competitive, closed, arid and nutrient-poor vegetation (Eriksson & Jakobsson 2000, Leishman 2001). Large-seeded seedlings have a better ability to colonise these sites than small-seeded seedlings (Leishman & Westoby 1994, Hodkinson *et al.* 1998, Kotorova & Lepš 1999). This is because they have more abundant resources of nutrients and energy than small-seeded seedlings. A trade-off

between seed size and seed number complicates the predictability of the influences of seed size on regeneration. A greater number of small seeds compared to large seeds may negate the positive effect of large seed size in the process of colonisation.

Diaspore morphology influences both seed dispersal and seedling recruitment. Many dispersal strategies have evolved: Diaspores are dispersed by wind, animals and ballistically (Willson & Traveset 2000). Many diaspores have structures that facilitate their movement by a certain vector. For instance, diaspores dispersed by wind often have wings or pappus, and externally dispersed diaspores have sticky hairs, hooks, burrs or other structures that facilitate adhesion in furs or feathers. These structures also influence the orientation of diaspores in the soil and/or reduce burial and hence also influence the success of seed germination (Harper *et al.* 1970, Peart 1979, 1981, 1984).

It is often assumed that species that spread effectively by vegetative means have a poorer ability to regenerate by seeds. However, many clonal species have persistent and large seed banks, and successful seedling recruitment takes place in suitable conditions (Eriksson 1992, Eriksson & Fröborg 1995). Wide genetic variation within clonal populations probably reflects the occurrence of seedling recruitment (Ellstrand & Roose 1987, Eriksson 1997). Furthermore, despite effective allocation to vegetative growth, the large size of clonal plants may result in a large number of flowers and seeds / m<sup>2</sup>. These features may make regeneration by seeds more important than is generally assumed.

Among the different growth forms, herbs and sedges tend to require light in the seed germination phase (Grime *et al.* 1981, Chambers *et al.* 1987, Grime *et al.* 1988, Schütz & Rave 1999). Thus, they are dependent upon gaps in their seedling recruitment. On the other hand, grasses tend to tolerate shade in the germination phase, and may hence have a good ability to recruit in closed vegetation.

## 2 Aims of the study

I studied regeneration by seeds in several different alpine plant communities. The main aims were to investigate the significance of regeneration by seeds, its influence on vegetation structure, and the effect of environmental heterogeneity on regeneration and vegetation structure in northern alpine areas. More specifically, the main aims were as follows:

1. To compare seed bank and seedling densities across several alpine plant communities and to find out whether these densities are related to altitude and the relative proportions of different regenerative groups, seed sizes and diaspore morphologies (I-III). The importance of bare ground, vegetation, bryophytes and litter in the determination of seedling densities was also analysed. I assumed that a) the relative proportions of plant traits should be associated with the characteristics of seed banks and seedlings, and b) the seed bank densities are higher on the lower than the higher slopes.
2. To find out the critical transitions in the regeneration pathway (III-IV,VI). I suggested that the transitions from the standing vegetation to the seed bank (III) and from the seed rain and the seed bank to the phase of seedling emergence (IV) are critical.
3. To study the influence of clonality, seed sizes, diaspore morphologies and growth forms on the process of regeneration (III, IV-V). I predicted that all plant traits have some influence on the pattern of regeneration.
4. To find out the influence of disturbances on the seedlings (I) and seedling emergence (IV). I assumed that disturbances increase seedling densities and the number of emerging seedlings.
5. To find out the role of seed-seedling conflicts in regeneration and in the determination of the spatial structure of standing vegetation. I assumed that the seed-seedling conflicts have an impact on the pattern of regeneration.

The detailed hypotheses are presented in the papers.

### 3 Material and methods

In this thesis, descriptive (I, II, VI) experimental field methods (IV-VI) and greenhouse experiments were used (III, VI). The data were tested by using several statistical and multivariate ordination methods. A general description is given here, while detailed information is given in the papers. The abbreviations for the plant communities in the papers I-III are explained in Table 1. The taxonomic nomenclature is according to Hämet-Ahti *et al.* (1998).

#### 3.1 Study area and study sites

This study was carried out at Kilpisjärvi in the subarctic area (69°01'N, 20°50'E) of northernmost Finland in the summers of 1995-1998. In the papers I-II, findings on four heaths, two meadows, five snowbeds and four naturally or anthropogenically severely disturbed sites were reported. The last group included two heaths trampled by humans, an area of patterned ground broken by thawing and freezing processes and a herb-rich talus slope disturbed by moving gravel. These severely disturbed plant communities have relatively undisturbed counterparts: EMP, CASS, GRBED and EUME, respectively (Table 1).

Other plant communities were also affected by disturbances, but their intensity was low. In study III, eight plant communities, namely CASS, EUBED, EUME, GRHE, MYRT, RANU, SAL and TALL, were studied (Table 1). The altitude of the study sites varied from 570 m to 950 m above sea level. The chosen sites represent a many-sided selection of plant communities in this study area.

In the studies reported in the papers IV-V, three meadows and three heaths were examined. Different regenerative strategies were dominant in these communities, which makes their comparison interesting. The meadows were rich communities dominated by a non-clonal, bunch-like grass, *Anthoxanthum odoratum*, and three non-clonal, large-leaved herbs, *Viola biflora*, *Taraxacum* spp. and *Alchemilla* spp. In the heaths, two strongly clonal dwarf shrubs, *Empetrum nigrum* and *Vaccinium myrtillus*, were the dominant species. All sites were disturbed slightly by reindeer. Melting water also broke the soil in the meadows. Both communities were common in the study area.



Three low herb snowbeds and three *Ranunculus glacialis* snowbeds were reported in paper VI. The low herb snowbeds were relatively closed, early melting plant communities dominated by *Viola biflora*, *Sibbaldia procumbens* and *Anthoxanthum odoratum*. This plant community consisted of a micro-mosaic of low mounds with high coverage of big mosses and long hollows with mats of crustaceous lichens and thin mosses and hepatics. These hollows were channels of melting water, and they were dry at mid-summer. The *Ranunculus glacialis* snowbeds were sparsely vegetated late melting communities, where *Cassiope hypnoides*, *Ranunculus glacialis* and *Carex bigelowii* were the dominant species of the field layer. The vascular plant cover was sparse, and crustaceous lichens and thin hepatics and mosses (*Lophozia* spp., *Gymnomitrium* spp., *Pohlia* spp.) were dominant in the ground layer. Many large rocks broke the soil, and patches of no plant cover were common.

### 3.2 Field sampling

In the papers I-III, twelve 0.8 m \* 0.8 m squares were systematically established along three parallel transects in every plant community. Limited resources did not allow replication (several sites / plant community), but the used sampling provide generalisations over a large number of plant communities. Despite the number of samples is low, in this approach of many plant communities the number is big enough to give a valid result of the relative variation of seed banks. The cover proportions of vascular plant species, bare ground and rocks were measured in addition to the densities of 0- to 3-year-old seedlings. The intensity of disturbances was classified into two classes: slight intensity = cover of bare ground less than 25%, and severe intensity = cover of bare ground more than 25%. All the variables mentioned above were used in the first paper of the study. In paper II, the cover of vascular plant species and the regenerative groups as well as the seedling densities and disturbance classes were used.

In the papers IV-V, seven 2m \* 2m plots with 0.25 m \* 0.25 m sized control, regeneration, seed bank and seed rain squares were established in early August 1997. Vegetation was removed from the regeneration and seed bank squares, and the seed bank squares were sheltered with fibre cloths to prevent seed rain. Seed traps made of green turf mats were established in the seed rain squares. The cover of vascular plants was estimated in August 1997, and seedling emergence was counted at the seed bank, regeneration and control squares in early August and September 1997 and in early July, August and September 1998. The seed traps were removed from the squares in the early summer of 1998, and seeds were counted by species in the laboratory.

Table 1. Abbreviations of the plant communities discussed in the papers I-III.

CASS	<i>Cassiope tetragona</i> - <i>Empetrum nigrum</i> - <i>Dicranum</i> heath
EMP	<i>Empetrum nigrum</i> - <i>Pleurozium schreberi</i> heath
EUBED	Eutrophic low herb snowbed
EUME	Eutrophic low herb meadow
GRHE	Siliceous low grass and sedge heath
GRBED	Siliceous low grass and sedge snowbed
MYRT	<i>Vaccinium myrtillus</i> - <i>Dicranum</i> heath
OXY	<i>Oxyria digyna</i> - <i>Gymnomitrium</i> snowbed
PATT	Patterned ground
RANU	<i>Ranunculus glacialis</i> - <i>Gymnomitrium</i> snowbed
SAL	<i>Salix herbacea</i> - <i>Cassiope hypnoides</i> snowbed
TALL	<i>Trollius europaeus</i> - <i>Geranium sylvaticum</i> tall-herb meadow
TALU	Slightly calcareous low herb talus slope
TRCASS	Trampled <i>Cassiope tetragona</i> heath
TREMP	Trampled <i>Empetrum nigrum</i> heath

In study VI, one 10 m \* 10 m plot with ten 60 cm \* 60 cm squares was established at every site. The randomly established squares included seven 15 cm \* 15 cm sub-squares for the estimation of the cover of vascular plants species, crustaceous lichens, moss and hepatic genera, field layer, ground layer, bare ground and rocks. Furthermore, three seed traps made of green turf mats (15 cm \* 15 cm) were established on the squares in the early August of 1998 and 1999 for the estimation of seed rain. The seed traps were removed from the squares after the snow melt in the years 1999 and 2000, and seeds were counted with the help of a preparation microscope in the laboratory. For the statistical analyses, mosses and hepatics were classified into two groups: small mosses and hepatics and big mosses and hepatics. The first group included *Pohlia* spp., *Lophozia* spp. and *Gymnomitrium* spp. The latter group, on the other hand, included *Sanionia* spp. and *Brachythecium* spp.

### 3.3 Seed bank experiments

For the third paper (III), seed bank samples were collected with a soil core (diameter 15.0 cm and depth 5.0 cm) from eight plant communities in early September of 1997. At the time of collection, seed germination had mostly taken place in the field, and current-year seeds had not yet dispersed. Thus, the densities of the seed banks were at their lowest, and the results reflected a persistent seed bank. After a period of stratification in a humidified cold room (two months at +5°C), the samples were spread as a 0.5 cm layer on autoclaved (24 hours in +150°C) gravel. During the two germination periods (1<sup>st</sup> Nov 1997- 30<sup>th</sup> May 1998 and 15<sup>th</sup> September-20<sup>th</sup> December 1998) intersected by the second stratification period, a photoperiod of 16 h of day light and 8 h of twilight was

maintained. Temperature varied diurnally, the minimum being +15°C (at twilight) and the maximum + 24°C (at daylight) in the first germination period. In the second germination period the minimum and maximum temperatures were + 10°C and +24°C, respectively. The samples were watered regularly, and the seedlings were counted and identified every second day. In study VI, seed bank samples were collected with a soil core (diameter 5.0 cm and depth 2.0 cm) in early August 1998. Thus, they also reflected the persistent part of the seed banks. The samples were stratified and germinated in conditions similar to those reported in paper III.

### 3.4 Measurements of plant traits

In the papers I-III and V, vascular plant species were classified into regenerative groups according to their ability to reproduce by vegetative means (Söyrinki 1938, Fröberg & Eriksson 1997). In the papers I-III, the system by Söyrinki (1938) was applied. The four strategies were: NV = no vegetative reproduction (organs for vegetative reproduction are lacking), NP = little, if any, vegetative reproduction, VI = ineffective vegetative reproduction, VE = effective vegetative reproduction. In paper V, a simpler subdivision into clonal and non-clonal plants was used. Clonal plants included the plants capable of effective vegetative reproduction, while the other plants were classified as non-clonal.

In the papers III-V, the following categories of diaspore morphology were used: 1. diaspores with no special structures for dispersal or other processes in recruitment, 2. diaspores with pappus, 3. diaspores with wings or fringes, 4. fleshy fruits and 5. diaspores with awns, hooks and/or calyx. 100 seeds / species were dried at +80°C for three days and weighed (III-V). The following seed weight classes were used: 1.  $\leq 0.1$  mg (small seeds), 2.  $> 0.1 - 0.5$  mg (intermediate-sized seeds), 3.  $> 0.5 - 1.0$  mg (intermediate-sized seeds), 4.  $> 1.0 - 5.0$  mg (large seeds).

In paper V, plants were subdivided into the following four growth forms: 1. herbs, 2. sedges, 3. grasses and 4. dwarf shrubs. Graminoids were subdivided into grasses and sedges because they have different seed germination requirements (Grime *et al.* 1981, Chambers *et al.* 1987, Grime *et al.* 1988, Schütz & Rave 1999). The proportions of these plant traits were calculated from the coverage of adults and densities of seeds and seedlings.

### 3.5 Statistics

Most of the statistical analyses were run using the SPSS software. Multivariate ordination analyses were run using CANOCO (II) and PC-ORD (III-IV and VI). The t-test (III) was used in the comparisons of two parameters if the pattern of data was normally distributed. In violated cases, the Mann-Whitney U-test (I, IV) and the Wilcoxon test (V) were used. In multiple comparisons, the 1-Way ANOVA (II) and repeated-measures ANOVA (IV-V) were used. In the case of non-parametric data, the Kruskal-Wallis test (I-II, IV-V), Friedman test (V) and Mann-Whitney U-test for multiple comparisons (I) were used. To

explore the influence of environmental parameters on the distribution of adults, seeds and seedlings, multiple linear stepwise regression analysis was applied (VI). Detrended correspondence analysis (DCA, II, IV) and non-metric multidimensional scaling (III) were used to investigate the floristic similarity between plant communities or phases in the regeneration pathway. To examine the influence of environmental variables on the species composition of different phases in the regeneration pathway, canonical correspondence analysis was used (CCA, VI). Spearman's correlation analysis (Chambers 1993) and Jaccard's similarity coefficients (Jongman *et al.* 1987) were used to analyse the floristic compositions between two phases within plant communities (II, IV). Spearman's correlation analysis was also used to test the correlations of seedling densities and seed bank densities with the relative proportions of regenerative groups, seed sizes, diaspore morphologies and altitude (I, III).

## 4 Results

### 4.1 Seed bank and seedlings across plant communities

Seedlings were abundant in many plant communities (I). Seedling densities were higher in snowbeds and meadows (range from 32.9 to 226.7 seedlings / m<sup>2</sup>) than in heath vegetation (range from 0.2 to 15.2 seedlings / m<sup>2</sup>). Seedling densities did not decrease with increasing altitude. There was a positive correlation between seedling densities and the coverage of plants with no ability or ineffective ability for vegetative reproduction. On the other hand, the correlation was negative between the seedling densities and the coverage of plants with an ability for effective vegetative reproduction.

The floristic similarity between the standing vegetation and the seedlings was low according to all analyses (II). The similarity index was highest (above 0.4) in the plant communities dominated by herbs and trailing dwarf shrubs and lowest (below 0.2) in the plant communities dominated by grass-like plants and dwarf shrubs (Jaccard's similarity coefficient). Only in four plant communities out of 15 were significant correlations found between the floristic compositions of the standing vegetation and the seedlings (Spearman's correlation analysis).

Across 15 plant communities, the first axis of standing vegetation and the second axis of seedlings resembled each other (DCA, II): both axes reflected differences in growth form contributions. The second axis of standing vegetation differentiated plant communities from each other in terms of snow cover persistence, nutrient status and altitude. The first axis of seedlings differentiated plant communities from each other in terms of nutrient status. The plant communities were more poorly differentiated in the phase of seedlings than in the standing vegetation. Furthermore, dwarf shrub heaths, siliceous grass and sedge heaths and siliceous low grass and sedge snowbeds were more heterogeneous (the squares were more widely spread) in the first phase than in the second one. The dominant species in these two phases of the regeneration pathway were different, as there were herbs with no ability, a possible ability and ineffective ability for vegetative reproduction among the seedlings and species with an ability for effective vegetative reproduction in the standing vegetation.

The seed bank densities ranged from 99 to 1109 viable seeds/ m<sup>2</sup> (III). *Phyllodoce caerulea*, *Cassiope tetragona*, *Carex bigelowii*, *Luzula* spp., *Gnaphalium supinum*, *Sibbaldia procumbens* and *Veronica alpina* were dominant in the seed banks. The seed bank densities were higher in the meadows, snowbeds and heaths on the lower slopes than in the snowbeds and heaths on the upper slopes. The seed bank densities decreased with increasing altitude. In the heaths, meadows and early melting snowbeds, the seed bank density was clearly higher than the seedling density. On the other hand, in the late melting snowbeds on the upper slopes, these densities were more or less comparable to each other.

The increasing coverage of plants with an ability for effective vegetative reproduction and large-seeded plants in the seed bank resulted in lower seedling densities. On the other hand, seedling densities increased with the increasing proportions of plants with ineffective vegetative reproduction and the diaspores with pappus in the seed banks. The seed banks of eight plant communities were less well differentiated than the standing vegetation and the phases of seedlings (non-metric multidimensional scaling). Within plant communities, the floristic similarities between the seed bank and the standing vegetation as well as between the seed bank and the seedlings were low (Jaccard's qualitative similarity coefficients, Spearman's correlation analysis). The taxa that appeared only in the standing vegetation tended to have large seeds, an ability for effective vegetative reproduction and appendaged diaspores. The taxa that occurred only in the seed bank had appendaged diaspores or small seeds, and the taxa that occurred only in the phase of seedlings commonly had appendaged diaspores.

## 4.2 Regeneration by seeds in alpine meadow and heath

The densities of seed rain, seed bank and seedling emergence in gaps and in closed vegetation were always clearly higher in the meadow than in the heath (IV). Only two seedlings and two species emerged in the heath.

In the meadow, the seed rain and the seed bank densities were comparable to each other (IV). In the heath, the seed rain density was clearly higher than the seed bank density. The seedling emergence rates in gaps and closed vegetation were comparable to each other in both plant communities. The dominant species in gaps and in closed vegetation differed from each other in the meadow. Three small-seeded herbs, *Cerastium* spp., *Veronica alpina* and *Gnaphalium supinum*, two graminoids, *Luzula* spp. and *Carex* spp., and one heavy-seeded herb characterised by diaspores with pappus, *Taraxacum* spp., were dominant in gaps. On the other hand, two heavy-seeded herbs, *Viola biflora* and *Taraxacum* spp., and two small-seeded herbs, *Gnaphalium supinum* and *Veronica alpina*, were most abundant among the emerged seedlings of closed vegetation.

The standing vegetation of the meadow was differentiated from the other phases of the regeneration pathway (Fig. 1a, detrended correspondence analysis, IV). A lack of floristic similarity between the standing vegetation and the other phases was obvious (Jaccard's similarity, Spearman's correlation). The taxa that showed a declining tendency from the standing vegetation to the other phases tended to have appendaged diaspores, large seeds and large adult sizes. On the other hand, the taxa that strengthened their position from the

standing vegetation to the other phases tended to have small seeds and small adult sizes. In the heath, the correlation between the standing vegetation and the seed rain was statistically significant.

The correlations between the consecutive phases were statistically significant only between the seed rain and the emergence of seedlings in gaps as well as between the seed bank and the seedling emergence in gaps (Fig. 1b, IV). The taxa with appendaged diaspores tended to deteriorate as they progressed from the seed rain to the seed bank as well as from the seed rain and the seed bank to the phases of seedling emergence. Larger-seeded herbs consolidated their position from the seed bank to the phase of seedling emergence in closed vegetation. The taxa that occurred only in the standing vegetation of the meadow and the heath had similar features as described in III. The taxa that did not occur after the phase of seed rain in the meadow tended to have small seeds. Since only two seedlings emerged in the heath, it was not possible to observe changes after the seed rain.

The spectra of diaspore morphology, growth forms and clonality were largely similar to each other in the phases of the meadow (Fig. 1a, V). Distinct variation only appeared in the spectra of seed size. In the standing vegetation and the seed bank, intermediate-sized seeds were most abundant. Intermediate-sized and small-sized seeds were dominant in the seed rain and in the phase of seedling emergence in gaps. Large seeds were dominant in the phase of seedling emergence of closed vegetation. In the heath, all spectra were similar in the standing vegetation and the seed rain. During the regeneration pathway, the relative proportions of all traits varied remarkably (Fig. 1b, V). However, in the cases of growth forms and diaspore morphology, other traits seemed to explain the changes. In both plant communities, the relative proportion of small seeds increased and that of large seeds decreased from the standing vegetation to the seed rain. Furthermore, in the meadow, the proportion of intermediate-sized seeds increased and the proportion of small seeds decreased from the seed rain to the seed bank. The proportion of clonal plants decreased from the standing vegetation to the seed rain, increased from the seed rain to the seed bank, decreased from the seed bank to the phase of seedling emergence (in closed vegetation), and increased from the phase of seedling emergence (in closed vegetation) to the standing vegetation. In the heath, the low density of seedlings gave no real opportunity to observe changes in the proportions.

### 4.3 Micro-scale variation in two snowbed communities

In the low herb snowbed, big mosses and hepatics had contrasting influences on the distributions of the field layer and, on the other hand, seedling emergence and seedling survival (VI). The increase in their coverage reduced the coverage of the field layer and had a positive influence on the densities of seedlings that emerged and survived. Furthermore, crustaceous lichens had a negative influence on the density of emerged seedlings. In the *Ranunculus glacialis* snowbed, there was a positive association between the coverage of crustaceous lichens and the density of seed rain. Big mosses and hepatics had a negative influence on the seed rain, and the coverage of small mosses and hepatics had a positive influence on the density of survived seedlings.

In *Gnaphalium supinum*, the influence of the micro-site started after the seed rain (VI). Adults and seedlings of *Gnaphalium supinum* benefited from both small and big mosses and hepatics, and the survived seedlings benefited from small mosses and hepatics. In the case of *Sibbaldia procumbens*, seed rain, emerged seedlings and adults concentrated at the least sheltered micro-sites, namely on bare ground and sites with small mosses and hepatics. On the other hand, adults and seedlings of *Viola biflora* avoided such micro-sites. The cover of big mosses and hepatics had a negative influence on the density of seed rain of *Ranunculus glacialis*. Micro-site had no influence on the other phases.

In the low-herb snowbed, real species-environment correlations occurred in all phases (Monte Carlo test of CCA, VI). The selection of important factors varied from phase to phase, though some factors had influences in several phases. The influence of small mosses and hepatics and bare ground was significant in all phases, and the field layer and crustaceous lichens had a significant influence on the distribution of species in the standing vegetation, the seed rain and the seedling emergence. Big mosses and hepatics had a statistically significant influence on the distribution of species in the standing vegetation, emerged seedling and survived seedlings. The variation of the proportions of species along the gradients and the species that indicated the extreme or intermediate parts of the gradients varied from phase to phase. The phases of emerged and survived seedlings resembled each other in these respects. The standing vegetation differed clearly from the other phases. In this phase, several strongly clonal species were differentiated from the other species and associated with the extreme parts of the gradients.

In the *Ranunculus glacialis* snowbed, a real species-environment correlation was only seen in the standing vegetation (Monte Carlo test of CCA, VI). The influences of the field layer and the big mosses and hepatics were strongest. *Cassiope hypnoides* benefited from the high coverage of the field layer in both phases. *Oxyria digyna* occurred at the opposite extreme of these gradients.

Seed bank densities were comparable to each other in the gaps and in the closed vegetation of the low herb snowbed (VI). In the *Ranunculus glacialis* snowbed, on the other hand, seed bank density was higher in closed patches than in gaps.



## 5 Discussion

### 5.1 Relationships between standing vegetation, seed bank and seedlings

Seed bank and seedling densities were remarkably high in many plant communities (I, III). This is contrary to the common assumption, which emphasises the minor importance of regeneration by seeds in northern and alpine areas. However, there are also reports that demonstrate effective generative reproduction. Niilo Söyrinki (1938), in the late 1930's, discovered total seedling densities that were commonly several hundreds or even thousands of seedlings per  $\text{m}^2$ , in the Petsamo District in subarctic Finland. Several decades later, Freedman *et al.* (1982) and McGraw and Shaver (1982) also reported high total seedling densities in the Arctic: at Ellesmere Island, High Arctic Canada, 13-5916 seedlings /  $\text{m}^2$ , and in Alaska, 35-3376 seedlings /  $\text{m}^2$ . Furthermore, the total densities of seed banks are commonly several hundreds or even thousands of viable seeds /  $\text{m}^2$  (Freedman *et al.* 1982, Fox 1983, Roach 1983, Chambers 1993, Semenova & Onipchenko 1993). In alpine areas, seedling survivorship may be high, commonly more than 50% after two growing seasons (Chambers *et al.* 1991), and remarkably large seed rain densities have been reported (Chambers 1993, Urbanska & Fattorini 2000). The seed bank densities at Kilpisjärvi were clearly higher than in the vicinity of Kilpisjärvi in subarctic Sweden (Diemer & Prock 1993, Molau & Larson 2000). The absence or very low density of low-statured species in the seed banks of the studied sites in subarctic Sweden may be related to the low intensity of grazing in this area compared to Kilpisjärvi. The low grazing intensity may be one reason for the very low seed bank densities in subarctic Sweden.

The seed bank densities decreased with increasing altitude (I, III). On the other hand, there was no correlation between the seedling densities and altitude. The first relationship is associated with the smaller amount and poorer quality of seeds on higher compared to lower slopes (Laine *et al.* 1995). However, the more open vegetation of the higher slopes provides suitable safe sites for seed germination and seedling recruitment and therefore results in the absence of an association between seedling densities and altitude.

The described associations of seedling densities with the proportions of regenerative groups in the standing vegetation and the seed banks reflect the poorer ability of strongly clonal plants to seedling recruitment compared to weakly clonal and aclonal ones (Eriksson 1992, II, III). The associations in floristic similarity between these phases reflect a similar phenomenon (II, III). The proportion of heavy seeds was high in the seed banks of heaths on the lower slopes, where seedling densities were low. These heaths are characterised by a thick moss cover, which hinders seedling recruitment of all species, even large-seeded ones.

Disturbances were not beneficial for seedling recruitment (I). Trampling and soil movement destroy standing vegetation, in both the field layer and the ground layer, and therefore reduce competitors of seedlings. This should result in higher seedling densities compared to closed vegetation, as reported by Tyler 1995, Kotorova & Lepš 1999 and Kiviniemi & Eriksson 1999. The results of these investigations, however, are based on post-disturbance circumstances, with seeds available via seed-producing plants and seed banks. At the disturbed sites reported in paper I, the disturbances were continuous and progressive. The soil was compact or unstable, which prevents seed entrapment and seedling recruitment.

The floristic similarity between the standing vegetation, the seed bank and the seedlings was low because of the changes in the success of certain plant traits during regeneration. Clonality, large and small seed sizes, appendaged diaspores and possibly narrow first leaves in seedlings limit the movement of plants from phase to phase in the regeneration pathway. Seedling recruitment is limited in clonal plants (Eriksson 1992). Small seeds accumulate in the seed bank more effectively than large seeds (Thompson *et al.* 1998), but large-seeded seedlings have a better ability to recruit at the phase of seedlings than small-seeded ones, especially in competitive, shaded, arid and nutrient-poor conditions (Eriksson & Jakobsson 2000, Leishman 2001). Appendaged diaspores seem to limit seed bank accumulation and seedling recruitment. Peart (1979, 1981, 1984) has shown that appendages have a significant influence on the seedling recruitment of grasses. Narrow first leaves also provide little chance for seedlings in the competitive circumstances of closed vegetation. The variation in adult size is a crucial determinant of the relationships between the standing vegetation and seedlings. In these plant communities, adult size is associated with an ability for vegetative reproduction. Thus, plants with an ability for effective vegetative reproduction increase their proportion from the phase of seedlings to the phase of standing vegetation, while non-clonal and weakly clonal species decrease their proportion. This was reflected in both the within-community relationships and the differences across plant communities (II).

The seed banks of eight plant communities were more similar to each other than the phases of seedlings and standing vegetation (III). The seed banks were at their poorest at the time of collection and reflected a persistent part of the seed banks. The importance of *Carex* spp. was notable in all seed banks, which also increased the floristic similarity between the seed banks. In the standing vegetation and among seedlings, there were no species that would have abundantly spread over the phases of seedlings and standing vegetation. *Carex* spp. includes *Carex bigelowii*. The seeds of this species may maintain their viability in the soil for up to 200 years (McGraw *et al.* 1991). This long-term accumulation of seeds in the soil is a probable reason for its notable importance even in communities where it has low coverage.

## 5.2 Characteristics of regeneration by seeds in meadow and heath

Regeneration by seeds in the meadow and the heath differed greatly from each other (IV). The trade-off between seed production and vegetative growth (Eriksson 1997) determines the abundance of dispersed seeds in plant communities. It explains the low seed rain density of heaths compared to meadows. The thick moss cover and drought hinder seedling emergence from the seed bank and prevent seed rain almost completely in the heath. On the other hand, the moist conditions of the meadow facilitate the emergence of large seedlings.

Schott & Hamburg 1997, Jensen 1998, Molau & Larson 2000 and Rabinowitz 1981 have documented a marked reduction in the number of seeds from the seed rain to the seed bank. This may sound illogical, because the seed banks include the seed rains of many years. However, there are several reasons for this relationship. Seed germination may be effective in the field, and seeds on or near the soil surface are exposed to seed predation and fluctuations of temperature and moisture and attacked by soil pathogens (Simpson *et al.* 1989, Schott & Hamburg 1997, Dalling *et al.* 1998, Hulme 1998). Furthermore, many seeds in the seed rain are transient and lose their viability within one year (Thompson *et al.* 1997). In the meadow, moist conditions facilitated seedling emergence, and seed bank accumulation was ineffective. This supports the previous results. In contrast, the relationship in the heath differed from these common observations. Because of the environmental obstacles (a thick moss cover and drought) to seed germination, the accumulation of the seed bank is effective in the heath.

Open gaps where seedlings can avoid competition with adults are assumed to be crucial for the emergence of seedlings (Gartner *et al.* 1986, Kiviniemi & Eriksson 1999). In the studied plant communities, however, seedling emergence was similar in gaps and in closed vegetation. In the heath, the drought in the gaps hinders seedling emergence equally effectively as the thick moss cover of the closed patches. In the meadow, a shift took place in the dominant taxa from gaps to closed vegetation. Two large-seeded herbs, *Viola biflora* and *Taraxacum* spp., were among the dominants in closed vegetation. The large seed size facilitates seedling emergence in the competitive circumstances of closed vegetation (Kotorova & Lepš 1999, Leishman & Westoby 1994). The emergence of all graminoid seedlings was reduced in closed vegetation, including the species with large seeds (*Carex* spp.) and *Anthoxanthum odoratum*, which has an equal capacity to germinate in dark and light conditions (Grime *et al.* 1988). Narrow first leaves of seedlings may be a feature that hinders their emergence in closed patches. Some small-seeded species also emerged abundantly in closed vegetation. Small-scale natural disturbances probably explain this.

The floristic similarity in the meadow was mostly low between the standing vegetation and the other phases in the regeneration pathway as well as between the consecutive phases in the regeneration pathway (IV). In the first case, the positive influences of adult size on the cover values and of seed number on the densities of seed rain, seed bank and emerged seedlings were the reasons for the low correlations. The tendency of appendaged diaspores to limit seed burial and, consequently, to leave seeds in the risky layers of the soil surface and the top layer of the soil (Peart 1984) was probably one reason for the low correlation that persisted from the seed rain until seedling emergence. The changes from

the seed bank to the seedling emergence of closed vegetation reflected the negative influence of small seed size on seedling emergence in competitive environments (Eriksson & Jakobsson 2000).

In the heath, because of poor seedling emergence, it was possible to compare only the standing vegetation and the seed rain. The results of detrended correspondence analysis reflected the variation in the dispersal ability of the dominant species. The majority of the fruits of *Empetrum nigrum* and *Vaccinium myrtillus* drop in the vicinity of their sources. On the other hand, the winged diaspores of *Betula nana* can disperse across long distances, and its diaspores may drop in places where *Betula nana* does not grow. The low number of species, the variable sizes of the species and poor seed dispersal probably resulted in the significant correlation between the standing vegetation and the seed rain in this community. Large-sized species may have more flowers and therefore more seeds / m<sup>2</sup> than small-sized species. A similar relationship was also found between the standing vegetation and the seedlings in this community (II).

The variation in the spectra of seed size between the phases in the regeneration pathway reflected a trade-off between seed size and seed number (Westoby *et al.* 1992, Henry & Westoby 2001) and a better ability of large-seeded seedlings to emerge in closed vegetation compared to small-seeded seedlings (Leishman & Westoby 1994, Hodkinson *et al.* 1998, Kotorova & Lepš 1999). The same was true of the changes of different seed sizes from phase to phase. Changes in the relative proportions of clonal and non-clonal plants reflected a trade-off between vegetative growth and seed production (Eriksson 1997) and a poor ability of clonal plants to recruit in closed populations (Eriksson & Fröberg 1996). Thus, these results strengthen the conclusions about the low floristic similarity between the phases during regeneration (IV).

### 5.3 Development of the spatial structure of standing vegetation

The influence of micro-sites on the distributions of seeds, seedlings and adults implies the presence of seed-seedling conflicts (VI). In the low-herb snowbed, secondary seed dispersal via melting water and strong wind were probably the reasons for the independence of the seed rain in relation to the micro-sites. However, micro-sites limit seedling emergence and seedling survival. Mosses and hepatics seem to provide suitable safe sites for these processes. Mosses and hepatics are known to stabilise the soil and to improve the soil moisture and nutrient conditions (Gartner *et al.* 1986, Sohlberg & Bliss 1987). In contrast, they seem to compete successfully with juveniles and adults, because an increase in their coverage results in a decrease in the field layer coverage. Thus, the process of seedling emergence and the growth and survival of juveniles and adults are the critical phases in this community, which limit the efficiency of regeneration by seeds. The critical nature of the first phase has been documented in some populations elsewhere (Houle 1995, Cuevar 2000). In the *Ranunculus glacialis* snowbed, three processes, seedling emergence, seedling survival and growth and survival of juveniles and adults appeared to be critical. Crustaceous lichens provided favourable substrates for seed rain but not for seedling emergence. Crustaceous lichens often grow on mats of *Cassiope hypnoides*. This species constituted most of the seed rain but had no seedlings. Since small mosses and hepatics stabilise the soil, they facilitate seedling survival. A likely

reason for the absence of association between the field layer and the micro-sites is the ability of clonal plants to spread via ramets to less favourable micro-sites (Stuefer *et al.* 1996, Stöcklin & Bäumler 1996).

In *Gnaphalium supinum*, the micro-sites limited seedling emergence, seedling survival and the cover of adults in a similar way. Seedling emergence was critical, and a probable reason for the concentration of seedling emergence among mosses and hepatics is the shelter they provide for the small-sized seedlings. The shoots of *Viola biflora* seedlings are long and their cotyledons are relatively wide and thin. This is probably why these seedlings avoid the most exposed, windy micro-sites. In the case of *Sibbaldia procumbens*, the same features probably made the survival of seedlings critical. The initial size of its seedlings is probably small enough to avoid the influence of drying wind in the phase of seedling emergence. However, its adults favour unsheltered micro-sites, probably because of the lesser competition. It was not possible to observe the fates of seedlings of *Ranunculus glacialis*.

In the low-herb snowbed, the phase of seedling emergence limited most the ability of the spatial vegetation structure to develop by generative means (CCA). The great importance of strongly clonal species in the standing vegetation resulted in a different pattern of this phase compared to the other phases. These species were concentrated in the extreme parts of the gradients and seemed to limit the recruitment of other species at these micro-sites. Thus, the infrequent pulses of seedling recruitment and clonal spreading have a crucial influence on the development of the spatial structure in this community. In the *Ranunculus glacialis* snowbed, it was not possible to conclude anything about the seed-seedling conflicts, since the gradients were rarely real.

## 6 Conclusions

I found the following answers to the questions I outlined for this thesis:

1. Seed bank densities decreased with altitude, but altitude had no influence on seedling densities. Seedling densities were high in the plant communities where plants with poor vegetative reproduction were abundant in the seed bank and in the standing vegetation. The correlation between the seedling densities and the relative proportion of large seeds in the seed banks was negative.
2. All transitions in the regeneration pathway limited regeneration by seeds. In the alpine meadow, only two relationships implied the minor obstacles against regeneration by seeds. In the heath, the transition from the seed rain and seed bank to seedling emergence was highly critical: despite the high seed rain and seed bank densities, only one seedling emerged. In the low-herb snowbed, the process of seedling emergence was most critical, and in the *Ranunculus glacialis* snowbed, three transitions, viz. seedling emergence, seedling survival and the survival of juveniles and adults, were most critical.
3. Clonality, large and small seed sizes and appendaged diaspores limited the movement of species from phase to phase in the regeneration pathway. In the meadow, the influences of plant size, seed size and diaspore morphology explained the low floristic similarity between the consecutive phases. The spectra of seed size varied clearly from phase to phase as well. The proportions of clonality, non-clonality, seed size, diaspore morphology and growth form varied, but the impacts of growth form and diaspore morphology usually seemed to be secondary.
4. Generally, disturbances facilitated effective regeneration by seeds in this area. Grazing resulted in large seed bank densities, and freezing and melting processes offered safe sites for seedling recruitment. However, seedling recruitment was not more abundant at severely disturbed sites than at relatively undisturbed ones. Furthermore, in the meadows, artificial gaps did not result in more abundant seedling emergence compared to closed vegetation. The meadows included species that emerge successfully in gaps, closed vegetation or both, and there was a shift in the species composition of seedlings from gaps to closed vegetation.

5. Seed-seedling conflicts limited the efficacy of regeneration by seeds in snowbed communities and lessened the impact of regeneration by seeds on the spatial structure of the standing vegetation.
6. All in all, this study shows that regeneration by seeds has, in favourable conditions, a significant impact on the dynamics and structure of alpine vegetation in the Subarctic.

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