

Characteristics of the seedling flora in alpine vegetation, subarctic Finland, II. Floristic similarity between seedling flora and mature vegetation

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We compared the floristic composition of the seedling flora and the mature vegetation in several alpine plant communities. First, we examined whether it is possible to predict the floristic composition of the seedling flora from the floristic composition of the mature vegetation. Second, we explored whether severe disturbances increase the floristic similarity between these two phases in the life-cycle. It is possible to make a rough prediction across the plant communities. This is because almost all taxa existing in the seedling flora are also present in the mature vegetation, and because the parallel changes in the floristic composition occur along DCA axes. The floristic similarity between the seedling flora and the mature vegetation within the plant communities was low. The variation in the qualitative similarity was closely related to the cover of the regenerative groups. On the other hand, the variation in the quantitative similarity was not related to these factors. In most cases the seedling flora and the mature vegetation were not more similar within the severely disturbed plant communities than within the relatively undisturbed ones.

Keywords: alpine vegetation, DCA, floristic similarity, regenerative groups, seedling flora, severe disturbances, Subarctic

INTRODUCTION

Seed and seedling dynamics of plant communities are most commonly studied by comparing seed bank and mature vegetation (e.g. Roach 1983,

Chambers 1993, Ungar & Woodell 1993, Looney & Gibson 1995, Holmes & Cowling 1997). Only few studies have analysed relationships between seedling flora and mature vegetation (Freedman *et al.* 1982, Piroznikow 1983, Leck & Simpson

1993, 1995). The seed bank, the seedling flora and the mature vegetation represent different phases in the life-cycle however, and they often differ in species composition (Freedman *et al.* 1982, Piroznikow 1983, Leck & Simpson 1993, Milberg 1993, Semenova & Onipchenko 1994, Leck & Simpson 1995). For this reason it is essential to understand the relationships between the seedling flora and the mature vegetation, and not only the relationships between the seed bank and the mature vegetation, in order to understand the seed regeneration patterns of the communities.

In this paper, we compare the floristic composition of the seedling flora to the floristic composition of the mature vegetation. The main questions to be considered are as follows: To what extent do the floristic composition of the seedling flora and the mature vegetation resemble each other? Is it possible to predict the seedling flora structure from the mature vegetation structure? We set out to answer these questions by studying these relationships both across and within the plant communities. Investigating the similarity across the plant communities reveals whether the community types differ as clearly in their seedling flora as in their mature vegetation and whether the same factors regulate the structures of these life-cycle phases. We assume that a rough prediction across the plant communities is possible, since all the species contributing to the seedling flora also contribute to the mature vegetation in these extreme northerly areas (Freedman *et al.* 1982). Furthermore, we assume that the similarity level within plant communities is related to the cover of regenerative groups in the mature vegetation. We justify the assumption on the grounds that in the mature vegetation an increase in the cover of the species reproducing mainly by seed should lead to an increase in their similarity, while an increase in the cover of the species reproducing mainly vegetatively should reduce this similarity. Neither analyses across the plant communities nor detailed comparisons of the seedling flora and the mature vegetation within plant communities have been performed previously.

The next question we asked was whether the mature vegetation and the seedling flora resemble each other more in severely disturbed sites than in relatively undisturbed ones. We assume that the similarity is higher in the severely dis-

turbed sites than in the relatively undisturbed ones. This is because disturbances often facilitate germination and seedling recruitment by providing better light, nutrient and temperature conditions than in the undisturbed sites (e.g. Amen and Bonde 1964, Reynolds 1984, Haggas *et al.* 1987, Chambers *et al.* 1991, Chambers 1995).

MATERIAL AND METHODS

Abbreviations and nomenclature

Abbreviations: DCA = detrended correspondence analysis, CASS = *Cassiope tetragona*-*Empetrum nigrum*-*Dicranum* heath, EMP = *Empetrum nigrum*-*Pleurozium schreberi* heath, EUBED = eutrophic low herb snowbed, EUME = eutrophic low herb meadow, GRHE = siliceous grass and sedge heath, GRBED = siliceous low grass and sedge snowbed, MYRT = *Vaccinium myrtillus*-*Dicranum* heath, NV = plants with no vegetative reproduction ability, OXY = *Oxyria digyna*-*Gymnomitrium* snowbed, PATT = patterned ground, RANU = *Ranunculus glacialis*-*Gymnomitrium* snowbed, SAL = *Salix herbacea*-*Cassiope hypnoides* snowbed, TALL = *Trollius europaeus*-*Geranium sylvaticum* tall herb meadow, TALU = slightly calcareous low herb talus slope, TRCASS = trampled *Cassiope tetragona* heath, TREMP = trampled *Empetrum nigrum* heath, VE = plants with effective vegetative reproduction ability, VI = plants with ineffective reproduction ability, VP = plants with the possibility for vegetative reproduction.

Nomenclature: Hämet-Ahti *et al.* (1998).

Study area and study sites

The study was carried out at Kilpisjärvi in the subarctic zone (69°01'N, 20°50'E) of northernmost Finland. The altitudes of the study sites varied from 570 m to 950 m (Table 1). Thus the vegetation of both low-alpine and mid-alpine zones were examined. There were four heaths (MYRT, EMP, CASS and GRHE), two meadows (TALL and EUME), five snowbeds (GRBED, EUBED, RANU, OXY and SAL) and four naturally or anthropogenically severely disturbed sites (TALU,

Table 1. The fifteen plant communities and their main characteristics in the summers of 1995–1996. COMM = plant community, CASS = *Cassiope tetragona*-*Empetrum nigrum*-*Dicranum* heath, EMP = *Empetrum nigrum*-*Pleurozium schreberi* heath, EUBED = eutrophic low herb snowbed, EUME = eutrophic low herb meadow, GRBED = siliceous low grass and sedge snowbed, GRHE = siliceous grass and sedge heath, MYRT = *Vaccinium myrtillus*-*Dicranum* heath, OXY = *Oxyria digyna*-*Gymnomitron* snowbed, PATT = patterned ground, RANU = *Ranunculus glacialis*-*Gymnomitron* snowbed, SAL = *Salix herbacea*-*Cassiope hypnoides* snowbed, TALL = *Trollius europaeus*-*Geranium sylvaticum* tall herb meadow, TALU = slightly calcareous low herb talus slope, TRCASS = trampled *Cassiope tetragona* heath, TREMP = trampled *Empetrum nigrum* heath.

COMM	Elevation m a.s.l.	Dwarf shrubs	Grass-like species	Herbs	Dominant taxa in the ground layer	Dominant taxa in the field layer	Disturbance factor
MYRT	600	20.0	0.4	0.2	<i>Dicranum</i> sp. (57.5%), <i>Lophozia</i> sp. (5.0%)	<i>Empetrum nigrum</i> (10.9%), <i>Vaccinium myrtillus</i> (3.4%)	Reindeer grazing, tracks, low intensity
EMP	650	41.7	2.7	0.1	<i>Pleurozium</i> sp. (35.6%), <i>Hylacomium</i> sp. (23.3%)	<i>Empetrum nigrum</i> (32.9%), <i>Betula nana</i> (7.4%)	Reindeer tracks, low intensity
CASS	900	24.6	1.9	0.01	<i>Dicranum</i> sp. (66.7%), <i>Barbilophozia</i> sp. (66.7%)	<i>Empetrum nigrum</i> (8.5%), <i>Cassiope tetragona</i> (12.4%)	Reindeer grazing, low intensity
GRHE	850	3.3	4.4	1.3	<i>Dicranum</i> sp. (14.3%), Crustaceous lichens (11.2%)	<i>Carex bigelowii</i> (2.9%), <i>Cassiope hypnoides</i> (1.9%)	Reindeer grazing, tracks, low intensity
GRBED	800	5.3	6.3	0.6	<i>Dicranum</i> sp. (37.8%), <i>Barbilophozia</i> sp. (11.7%)	<i>Carex bigelowii</i> (3.9%), <i>Phyllococe caerulea</i> (2.3%)	Thawing and freezing processes, low intensity
EUBED	820	4.4	11.2	13.0	<i>Sanionia</i> sp. (14.8%), <i>Dicranum</i> sp. (14.3%)	<i>Viola biflora</i> (5.3%), <i>Carex bigelowii</i> (3.6%)	Reindeer grazing, channels of melting water, low intensity
RANU	845	14.2	1.8	3.1	<i>Gymnomitron</i> sp. (14.7%), <i>Lophozia</i> sp. (11.7%)	<i>Cassiope hypnoides</i> (13.6%), <i>Ranunculus glacialis</i> (1.5%)	Thawing and freezing processes, low intensity
OXY	820	0.9	0.9	3.2	<i>Gymnomitron</i> sp. (22.5%), <i>Barbilophozia</i> sp. (11.8%)	<i>Oxyria digyna</i> (1.6%)	Thawing and freezing processes, low intensity
SAL	800	12.8	1.4	3.6	<i>Lophozia</i> sp. (14.3%), <i>Dicranum</i> sp. (6.2%)	<i>Cassiope hypnoides</i> (9.6%), <i>Salix herbacea</i> (3.7%)	Thawing and freezing processes, low intensity
TALL	560	1.8	16.7	26.7	<i>Pleurozium</i> sp. (5.6%), <i>Barbilophozia</i> sp. (1.3%)	<i>Trollius europaeus</i> (6.7%), <i>Geranium sylvaticum</i> (4.7%)	Reindeer grazing, low intensity
EUME	570	1.1	5.7	9.9	<i>Polytrichum</i> sp. (9.8%), <i>Sanionia</i> sp. (9.8%)	<i>Viola biflora</i> (5.2%), <i>Carex bigelowii</i> (2.3%)	Reindeer grazing, tracks, low intensity
TREMP	650	9.4	2.8	0.03	<i>Polytrichum</i> sp. (1.1%)	<i>Empetrum nigrum</i> (6.7%), <i>Carex bigelowii</i> (1.0%)	Human trampling, severe intensity
TRCASS	950	5.8	2.9	0.0	<i>Dicranum</i> sp. (5.1%), <i>Pohlia</i> sp. (1.4%)	<i>Betula nana</i> (2.8%), <i>Festuca ovina</i> (2.2%)	Human trampling, severe intensity
PATT	800	7.8	2.5	1.5	<i>Barbilophozia</i> sp. (16.6%), <i>Polytrichum</i> sp. (6.2%)	<i>Phyllococe caerulea</i> (3.1%), <i>Salix herbacea</i> (2.2%)	Thawing and freezing processes, severe intensity
TALU	570	0.1	2.2	4.3	<i>Lophozia</i> sp. (0.04%), <i>Bynum</i> sp. (0.04%)	<i>Taraxacum</i> sp. (1.0%), <i>Campanula rotundifolia</i> (0.8%)	Falling gravel, reindeer trampling, severe intensity

PATT, TREMP, TRCASS; Table 1, Appendices 1 and 2). The study sites are described in more detail in Welling and Laine (2000).

Sampling

At the 15 study sites, three parallel 7-m-long transects were established three metres from each other. Along every transect, four 80 cm × 80 cm squares (Oksanen & Virtanen 1995) were placed systematically one metre from each other.

Cover values of vascular plant species and growth forms (dwarf shrubs, herbs and grass-like species) were recorded visually, in addition to the cover values for bare ground. Seedlings about 0 to 3 years old were counted and the species identified. The development of stage was estimated as proposed by Wager (Wager 1938, Freedman *et al.* 1982). The intensity of disturbances was classified in the following way: low intensity = cover of bare ground is less than 25%, severe intensity = cover of bare ground is more than 25%. In the classification of the species to the regenerative groups the system by Söyrinki (1938) was used. Sampling is described in more detail in Welling and Laine (2000).

Statistics

Detrended correspondence analysis based on CANOCO 2.1 (Ter Braak 1988) was used in the analyses across the plant communities. The analyses were carried out with the downweighting of rare species, no transformations and 4th order polynomial detrending. Four taxa (*Vaccinium myrtillus*, *V. vitis-idaea*, *Pyrola* sp. and *Rumex acetosa*) were deleted from the analysis of the seedling flora because of very low frequencies, and ten quadrats were rejected because of the absence of seedlings. We did not include EMP in the analyses either, because only one seedling existed at the site. Some species of the seedling flora could be identified only at the genus level, and these were treated collectively in both the seedling flora and the mature vegetation. The correlations between the site scores of the mature

vegetation and the seedling flora as well as between the species weights were analysed with the Spearman's rank correlation test. Only those species existing in both life-cycle phases were included in the analysis of the species weights. The analysis of the data with all species was not accepted because it would have placed too much emphasis on the species with both no seedlings and very low weights in the mature vegetation.

Several similarity analyses within plant communities were carried out. Both qualitative and quantitative Jaccard's similarity indices (Jongman *et al.* 1987) were calculated according to the equation:

$$SJ = c/(A + B - c), \quad (1)$$

where A is total number of species in the mature vegetation, B is total number of species in the seedling flora, and c is number of species shared by the mature vegetation and the seedling flora. The equation for the quantitative index is:

$$SR_{ij} = \sum_k Y_{ki} Y_{kj} / (\sum_k Y_{ki}^2 + \sum_k Y_{kj}^2 - \sum_k Y_{ki} Y_{kj}) \quad (2)$$

where Y_{ki} is abundance of the k -th species in the mature vegetation, Y_{kj} is abundance of the k -th species in the seedling flora, and $Y_{ki} Y_{kj}$ is abundance of species shared by the mature vegetation and seedling flora. For the quantitative analysis the data of the mature vegetation and seedling flora were transformed to comparable percentage values, i.e. the sums of the densities and covers were 100% at each site. The variation in the qualitative and quantitative similarity between the plant communities was analysed with One-Way ANOVA. The Tamhane's test was used as a post-hoc test because of high variation in variances. EMP was not included in the analyses because the value of its variance was 0.0. The Spearman's rank correlation analysis was carried out with the ranks of the averages for species existing in both the seedling flora and the mature vegetation (Chambers 1993). The same analysis was used for the similarity coefficients and the relative cover of the regenerative groups. In the comparison of the similarities between the severely disturbed plant communities and their relatively undisturbed counterparts the t -test was applied.

RESULTS

Similarity within plant communities

In general, both qualitative and quantitative similarity coefficients between the seedling flora and the mature vegetation were low (Table 2). The variations between the ten plant communities were statistically highly significant ($F = 19.334$, $p < 0.001$ in the qualitative similarity and $F = 5.073$, $p < 0.001$ in the quantitative similarity, respectively, according to One-Way ANOVA). The lowest qualitative similarity coefficients (less than 0.2) were obtained in the plant communities dominated by grass-like species and dwarf shrubs (GRHE,

MYRT and GRBED) while the coefficients were highest (more than 0.4) in the plant communities dominated by herbs and trailing dwarf shrubs (OXY, RANU and EUME, Table 2A). By contrast, in the comparison of the quantitative similarity there was no differentiation because of different growth form contributions (Table 2B). The Tamhane's test showed few statistically significant differences between the communities. The correlations between the relative abundances of the species existing in both the mature vegetation and the seedling flora were statistically slightly significant ($p < 0.05$) in only four plant communities: MYRT, OXY, RANU and EUME (Table 3).

When exploring the factors regulating the

Table 2. The comparison of (A) qualitative similarity and (B) quantitative similarity of 10 plant communities. CASS = *Cassiope tetragona-Empetrum nigrum-Dicranum* heath, EUBED = eutrophic low herb snowbed, EUME = eutrophic low herb meadow, GRBED = siliceous low grass and sedge snowbed, GRHE = siliceous grass and sedge heath, MYRT = *Vaccinium myrtillus-Dicranum* heath, OXY = *Oxyria digyna-Gymnomitrium* snowbed, RANU = *Ranunculus glacialis-Gymnomitrium* snowbed, SAL = *Salix herbacea-Cassiope hypnoides* snowbed, TALL = *Trollius europaeus-Geranium sylvaticum* tall herb meadow. The means and the standard errors are presented. The One-Way ANOVA and the Tamhane's post hoc-tests were used. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = not significant.

		MYRT	CASS	GRHE	GRBED	EUBED	RANU	OXY	SAL	TALL	EUME
(A)		0.11 (0.04)	0.26 (0.04)	0.10 (0.02)	0.17 (0.02)	0.30 (0.02)	0.46 (0.03)	0.48 (0.04)	0.23 (0.03)	0.20 (0.02)	0.43 (0.04)
MYRT	0.11 (0.04)	ns	ns	ns	ns	**	***	***	ns	ns	***
CASS	0.26 (0.04)	ns	ns	ns	ns	ns	*	*	ns	ns	ns
GRHE	0.10 (0.02)	ns	ns	ns	ns	***	***	***	*	ns	***
GRBED	0.17 (0.02)	ns	ns	ns	ns	**	***	***	ns	ns	**
EUBED	0.30 (0.02)	**	ns	***	**	ns	**	*	ns	ns	ns
RANU	0.46 (0.03)	***	*	***	***	**	ns	ns	***	***	ns
OXY	0.48 (0.04)	***	*	***	***	*	ns	*	**	***	ns
SAL	0.23 (0.03)	ns	ns	*	ns	ns	***	**	ns	ns	ns
TALL	0.20 (0.02)	ns	ns	ns	ns	ns	***	***	ns	ns	*
EUME	0.43 (0.04)	***	ns	***	**	ns	ns	ns	ns	*	ns
(B)		0.32 (0.10)	0.31 (0.07)	0.02 (0.01)	0.17 (0.07)	0.10 (0.02)	0.12 (0.03)	0.32 (0.06)	0.11 (0.03)	0.19 (0.03)	0.40 (0.06)
MYRT	0.32 (0.10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CASS	0.31 (0.07)	ns	ns	*	ns	ns	ns	ns	ns	ns	ns
GRHE	0.02 (0.01)	ns	*	ns	ns	ns	ns	*	ns	**	**
GRBED	0.17 (0.07)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
EUBED	0.10 (0.02)	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
RANU	0.12 (0.03)	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
OXY	0.32 (0.06)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SAL	0.11 (0.03)	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
TALL	0.19 (0.03)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
EUME	0.40 (0.06)	ns	ns	**	ns	*	*	ns	*	ns	ns

similarity patterns described above, there were statistically significant positive correlations between the qualitative similarity coefficients and the cover (%) of the species characterized by lacking vegetative reproduction ability or ineffective vegetative reproduction ability ($p < 0.05$, Table 4). The correlation was negative between the qualitative similarity and cover percentages of the species with an ability for effective vegetative reproduction ($p < 0.001$). In contrast, there were no statistically significant correlations between the quantitative similarity coefficients and the cover percentages of the regenerative groups.

In most cases the mature vegetation and the seedling flora were not any more similar at two severely disturbed sites than in their relatively undisturbed counterparts (Fig. 1). Only in TREMP both qualitative and quantitative similarity were significantly higher than in EMP ($p < 0.001$ and $p < 0.01$, respectively). Furthermore, in PATT qualitative similarity was significantly higher ($p < 0.01$) than in GRBED.

Similarity across plant communities

The eigenvalues of the first and second axes in the ordinations of the mature vegetation and the seedling flora were high (Fig. 2, 0.841 and 0.586 in the mature vegetation and 0.864 and 0.659 in

the seedling flora), which indicates high power in demonstrating the floristic variation in the squares. On the first axis of the mature vegetation dwarf shrub heaths and herb-rich plant communities were clearly separated from each other with grass-like species-dominated plant communities intermediate between them (Fig. 2a). Thus the axis demonstrates a difference in growth form contributions. The second axis demonstrates differences in snow-cover persistence, nutrient status and altitude. In the ordination of the seedling flora the most powerful axis separated poor plant communities from eutrophic herb-rich plant communities indicating a difference in nutrient status (Fig. 2b). The second axis separated the herb-rich plant communities and the dwarf shrub heaths from each other, with the grass-like species dominated communities intermediate between them. The seedling flora of SAL was now among the “calcareous herb-rich plant communities with intermediate snow cover” in the mature vegetation ordination instead of “poor herb-rich plant communities with long persistent snow cover”. Several quadrats of OXY were also intermediate between the two herb-rich plant community groups. The second axis separated poorly herb-rich plant communities from the grass-like species-dominated communities. In addition, the “dwarf shrub heaths” and “grass-like species-dominated communities” were more heterogeneous in structure

Table 3. Correlations between relative species cover in the seedling flora and the mature vegetation. Only the species existing in both life-cycle phases were included in the Spearman's rank correlation analyses. * = $p < 0.05$, ns = not significant. N = the number of species shared by the seedling flora and the mature vegetation.

Plant community	Species number (N)	Correlation
<i>Vaccinium myrtillus</i> - <i>Dicranum</i> heath	6	0.94*
Trampled <i>Empetrum nigrum</i> heath	5	0.10 ns
<i>Cassiope tetragona</i> - <i>Empetrum nigrum</i> heath	5	0.50 ns
Trampled <i>Cassiope tetragona</i> heath	2	
Siliceous grass and sedge heath	8	-0.20 ns
Siliceous grass and sedge snowbed	14	0.16 ns
Patterned ground with low grasses and sedges	10	0.37 ns
Eutrophic low herb snowbed	11	0.30 ns
<i>Ranunculus glacialis</i> - <i>Gymnomitrium</i> snowbed	10	0.59*
<i>Oxyria digyna</i> - <i>Gymnomitrium</i> snowbed	12	0.60*
<i>Salix herbacea</i> - <i>Cassiope hypnoides</i> snowbed	7	0.47 ns
<i>Trollius europaeus</i> - <i>Geranium sylvaticum</i> -tall herb meadow	12	-0.12 ns
Eutrophic low herb meadow	22	0.37*
Slightly calcareous low herb talus slope	15	0.23 ns

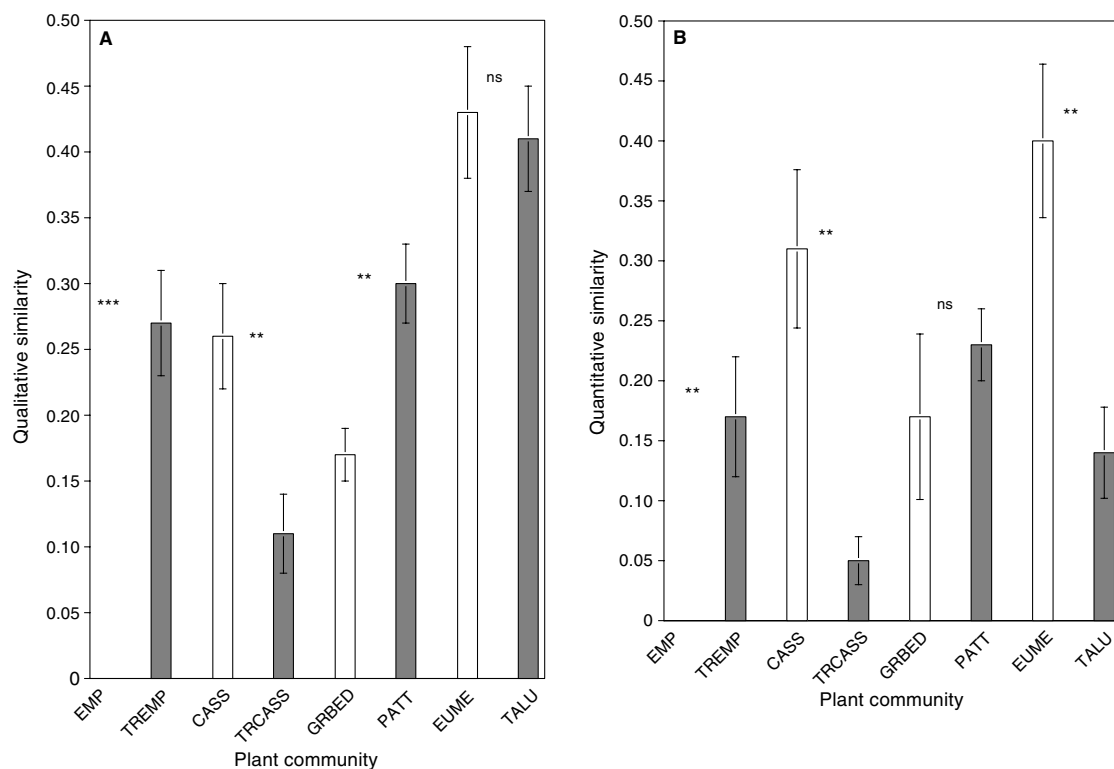


Fig. 1. — A: Mean Jaccard's qualitative similarity coefficients. — B: mean Jaccard's quantitative similarity coefficients between the mature vegetation and the seedling flora. White bars= relatively undisturbed vegetation, grey bars = severely disturbed vegetation. CASS = *Cassiope tetragona-Empetrum nigrum-Dicranum* heath, EMP = *Empetrum nigrum-Pleurozium schreberi* heath, EUME= eutrophic low herb meadow, GRBED = siliaceous low grass and sedge snowbed, PATT= patterned ground, TALU = slightly calcareous low herb talus slope, TRCASS= trampled *Cassiope tetragona* heath, TREMP= trampled *Empetrum nigrum* heath. ** = $p < 0.001$, ns = not significant.

than in the mature vegetation. The standard deviations in the seedling flora ordination (3.44 on the first axis and 8.21 on the second) were higher than in the mature vegetation ordination (2.52 and 3.35, respectively), which indicated higher overall heterogeneity in the seedling flora. The correlation between the first axes of the seedling flora and mature vegetation ordinations was positive and statistically significant ($r_s = 0.75$, $p < 0.01$, $n = 158$), but that between the second axes was negative and statistically significant ($r_s = -0.34$, $p < 0.01$, $n = 158$).

The correlation between species weights was statistically negligible (the Spearman's rank correlation analysis, $r_s = 0.57$, $n = 42$). Only nine species out of forty had approximately the same ranks in both the seedling flora and the mature

vegetation (Table 5): *Astragalus alpinus*, *Hieracium alpina*, *Potentilla crantzii*, *Silene acaulis*, *Taraxacum* sp., *Viola biflora*, *Agrostis mertensii*, *Anthoxanthum odoratum* and *Vahlodea atropur-*

Table 4. Correlations between the similarity coefficients and relative covers of the regenerative groups in the mature vegetation. The Spearman's rank correlation analysis was used; $n = 15$. * = $p < 0.05$, ** = $p < 0.01$, ns = not significant.

Regenerative group	Qualitative similarity	Quantitative similarity
NV	0.615*	0.392 ns
VP	0.191 ns	0.148 ns
VI	0.607*	0.092 ns
VE	-0.652**	-0.358 ns

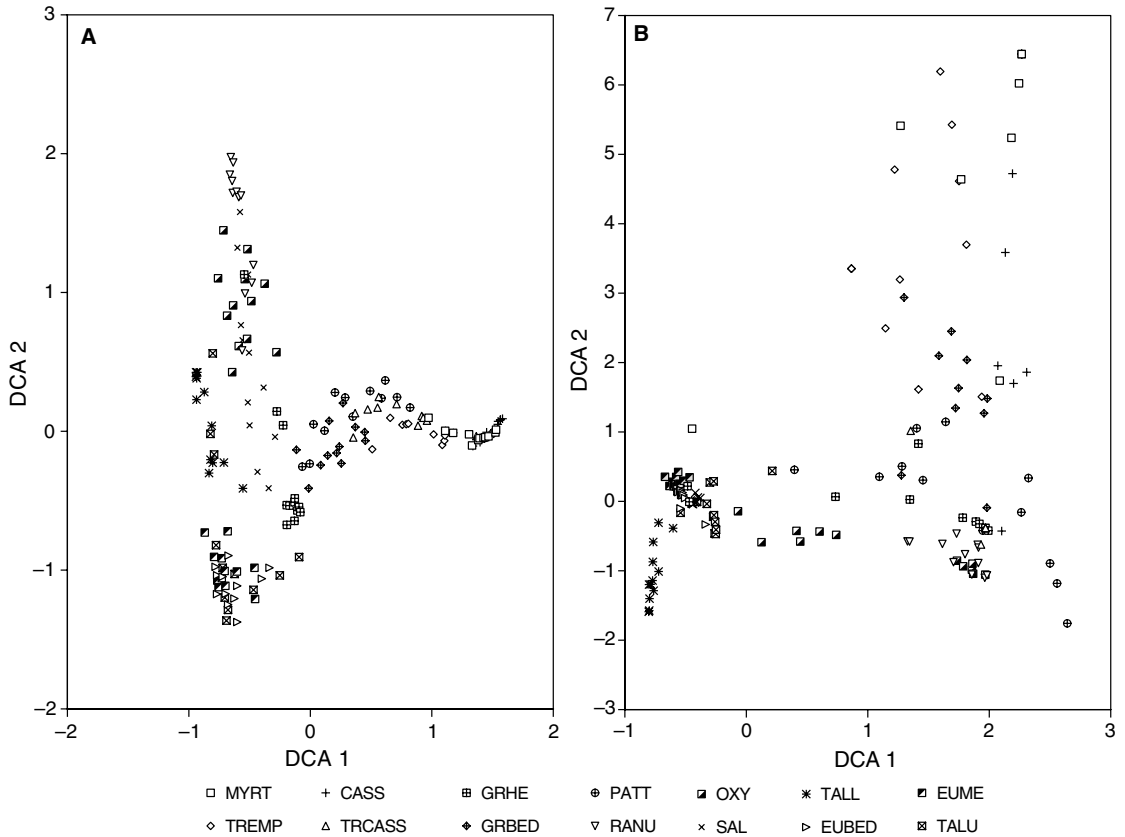


Fig. 2. Ordination of the squares, based on (A) cover percentages of species in the mature vegetation, and (B) seedling densities in the seedling flora.

purea. The dominants of the seedling flora were usually herbs by lacking vegetative reproduction ability, a possible vegetative reproduction ability or ineffective vegetative reproduction ability: *Cardamine bellidifolia*, *Cerastium* sp., *Gnaphalium supinum*, *Oxyria digyna*, *Ranunculus glacialis*, *Sibbaldia procumbens*, *Taraxacum* sp. and *Veronica alpina*. The weights of one genus, *Cerastium* sp., and four species, *Gnaphalium supinum*, *Sibbaldia procumbens*, *Veronica alpina* and *Viola biflora*, accounted for 68% of all the species weights in the seedling flora. In the mature vegetation, most of the dominants have an ability for effective vegetative reproduction. Only one species (*Euphrasia frigida*), existed in the seedling flora but not in the standing vegetation.

DISCUSSION

Similarity across the plant communities

The seedling flora was related to the mature vegetation across all 14 plant communities. This is because almost all taxa existing in the seedling flora also were present in the mature vegetation and because parallel changes in the floristic composition take place along the axes. A similar relationship has been observed between seed bank and mature vegetation in alpine areas and is based on the poor species and life-strategy pools of these areas (Diemer & Prock 1993, Chambers 1997).

As demonstrated, the seedling flora pattern is more mixed and heterogeneous across the plant

communities than the mature vegetation pattern. In SAL the high densities of *Gnaphalium supinum* and *Sibbaldia procumbens* seedlings, the absence of *Salix herbacea* and *Cassiope hypnoides* seed-

lings and the low species richness probably lead to the fact that the seedling flora is among the "herb-rich plant communities with intermediate snow-cover" instead of the "snowbeds with long

Table 5. Weighted averages and ranks of the seedling densities and the adult cover percentages.

Species	Reg. group	Weight in mature vegetation	Weight in seedling flora	Rank in seedling flora	Rank in mature vegetation
<i>Betula nana</i>	VE	88.0	3.7	3	33
<i>Cassiope hypnoides</i>	VE	324.6	2.2	1	40
<i>Cassiope tetragona</i>	VP	170.4	140.6	28	38
<i>Empetrum nigrum</i>	VE	328.2	123.4	26	41
<i>Phyllodoce caerulea</i>	VP	93.0	76.5	21	35
<i>Alchemilla</i> sp.	NV	27.6	7.4	6	22
<i>Antennaria</i> sp.	VE	25.7	9.6	7	21
<i>Astragalus alpinus</i>	VE	6.5	4.9	5	9
<i>Campanula rotundifolia</i>	VE	10.3	120.4	25	11
<i>Cardamine bellidifolia</i>	NV	1.4	228.2	30	6
<i>Cerastium</i> sp.	VP	13.6	1 119.6	37	15
<i>Geranium sylvaticum</i>	NV	44.8	7.4	6	26
<i>Gnaphalium supinum</i>	VI	52.5	3 967.4	40	29
<i>Hieracium</i> sp.	NV	10.9	37.5	17	12
<i>Hieracium alpina</i>	NV	20.9	40.7	18	19
<i>Minuartia biflora</i>	NV	0.4	18.8	11	3
<i>Oxyria digyna</i>	VP	38.5	323.3	32	25
<i>Potentilla crantzii</i>	VP	12.5	22.0	15	14
<i>Ranunculus acris</i>	VP	11.1	184.0	29	13
<i>Ranunculus glacialis</i>	NV	17.3	507.6	34	16
<i>Ranunculus nivalis</i>	NV	0.8	17.5	10	4
<i>Ranunculus pygmaeus</i>	NV	0.01	90.0	24	1
<i>Saussurea alpina</i>	VE	23.8	21.9	14	20
<i>Sibbaldia procumbens</i>	VP	46.1	1 028.5	36	27
<i>Silene acaulis</i>	NV	0.4	3.4	2	2
<i>Solidago virgaurea</i>	VP	59.9	17.3	9	30
<i>Taraxacum</i> sp.	NV	49.2	346.1	33	28
<i>Tofieldia pusilla</i>	VP	2.1	76.9	22	7
<i>Trollius europaeus</i>	NV	73.2	18.9	12	32
<i>Veronica alpina</i>	VI	8.8	1 337.6	39	10
<i>Viola biflora</i>	NV	166.1	1 309.4	38	36
<i>Agrostis mertensii</i>	VP	25.7	57.5	20	21
<i>Anthoxanthum odoratum</i>	VI	92.7	234.7	31	34
<i>Carex</i> sp.		19.6	10.9	8	18
<i>Carex bigelowii</i>	VE	222.5	20.5	13	39
<i>Carex lachenalii</i>	VP	17.6	134.7	27	17
<i>Deschampsia flexuosa</i>	VE	169.9	20.5	13	37
<i>Festuca ovina</i>	VP	67.6	81.5	23	31
<i>Juncus trifidus</i>	VI	31.0	34.5	16	23
<i>Luzula</i> sp.	VI	31.7	649.5	35	24
<i>Trisetum spicatum</i>	VP	2.7	44.0	19	8
<i>Vahlodea atropurpurea</i>	VP	0.9	4.7	4	5

persistent snow-cover". Very low seedling density and species richness lead to highly heterogeneous seedling floras in the "dwarf shrub heaths" and "grass-like species-dominated plant communities". In addition, heavily weighted averages of three taxa in the seedling flora, namely *Gnaphalium supinum*, *Sibbaldia procumbens* and *Cerastium* sp., lead to the mixed pattern.

Similarity within the plant communities

The factors that affect germination and survival can be species specific life-history characteristics (Chambers 1993) and environmental conditions (Chambers 1991, 1995). Chambers (1993) demonstrated how the similarity between the seed bank and the mature vegetation is determined by life-history strategies of species in the mature vegetation. The same explanation is found in the mature vegetation-seedling flora relationships. The increase of the cover of the species with no vegetative reproduction ability and those with ineffective vegetative reproduction ability in the mature vegetation lead to the increase in the qualitative similarity. In contrast, species with effective vegetative reproduction ability produce low seedling densities or no seedlings at all, and the increase of their covers in the mature vegetation leads to the decrease of the qualitative similarity.

The results for severely disturbed plant communities are not in agreement with earlier reports showing better conditions for seedling recruitment in disturbed communities than in undisturbed communities (Chambers *et al.* 1991, Chambers 1995). In TRCASS the mature phases are dominated by dwarf shrubs from the period preceding trampling. On the other hand, *Luzula* sp. dominates the seedling flora. Continued heavy trampling probably prevents their effective recruitment to the mature vegetation. Also the compactness of heavily trampled tracks may prevent seed entrapment. In TALU, continued severe disturbances caused by the moving substrate has probably led to the low similarity. On the other hand, in PATT the high micro-scale heterogeneity of the growing substrates may have led to the greater similarity. This is because there are micro-sites suitable for the establishment of the species with differing requirements. In addition, micro-scale barriers and

depressions of the site may facilitate seed entrapment. And in EMP thick moss carpet prevents seedling recruitment almost completely. This negative effect of moss cover has been demonstrated in more southern areas (van Tooren 1990, Rusch & Fernandez-Palacios 1995).

The low correlations between the relative species contributions to the seedling floras and the mature vegetations and between the quantitative similarity coefficients and the cover of the regenerative groups indicate that complex interactions between populations characterised by seedling and adult characteristics of many kinds (morphology and size), seedling density and survival patterns affect the discrimination between the life-cycle phases. In order to construct a profound synthesis of the relationships between the seedling flora and the mature vegetation, these characteristics and their connections with environmental factors should be investigated in the context of particular plant communities. In addition, seedling establishment investigations should be carried out in order to evaluate the extent to which seedlings contribute to the maintainance of the populations and the plant communities.

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Appendix 1. Continued.

Species	1	2	Plant community															
			EUBED	EUME	SAL	TALU	RANU	OXY	PATT	TALL	GRBED	GRHE	TREMP	MYRT	CASS	TRCASS	EMP	
<i>Ranunculus nivalis</i>	SA	NV	0.1	0.1				0.01										
<i>Ranunculus pygmaeus</i>	SA	NV					0.01	0.02										
<i>Rhodiola rosea</i>	SA	VP	0.01															
<i>Rumex acetosa</i>	?	NV				0.04				0.3								
<i>Saussurea alpina</i>	SR	VE	0.1	0.1						2.2								
<i>Sibbaldia procumbens</i>	SA	VP	1.5	0.7	0.8	0.3	0.4	0.1	0.04	0.04	0.01	0.01						
<i>Silene acaulis</i>	SA	NV							0.2									
<i>Solidago virgaurea</i>	SA	VP	0.1	0.8		0.01		0.1	0.04	3.9	0.03	0.1	0.01	0.02				
<i>Taraxacum</i> sp.	SA	NV	1.8	1.3		1.0				0.1								
<i>Thalictrum alpinum</i>	SA	VE	0.4							0.01								
<i>Tofieldia pusilla</i>	SA	VP							0.5									
<i>Trientalis europaea</i>	SR	VE									0.1							
<i>Trollius europaeus</i>	SA	NV		0.1						6.7								
<i>Veronica alpina</i>	SA	VI	0.4	0.2		0.1	0.01	0.03	0.01	0.01								
<i>Viola biflora</i>	SA	NV	5.3	5.2		0.2				3.1								
Grass-like plants																		
<i>Agrostis mertensii</i>	?	VP	1.4	0.02	0.2			0.03	0.4		0.1							
<i>Anthoxanthum odoratum</i>	SA	VI	3.1	2.1	0.1	0.8				1.7		0.01						
<i>Calamagrostis</i> sp.		VE									0.3		0.1		1.0	0.1		
<i>Calamagrostis lapponica</i>	SR	VE	0.04								0.01	0.02	0.04					2.6
<i>Calamagrostis purpurea</i>	NS	VE								1.3								
<i>Calamagrostis stricta</i>	SR	VE									0.04							
<i>Carex</i> sp.								0.01		2.9								
<i>Carex bigelowii</i>	SA	VE	3.6	2.3	1.1		0.2		0.9	1.3	3.9	2.9	1.04	0.4	1.0			
<i>Carex brunnescens</i>	SA	VP							0.04									
<i>Carex lachenalii</i>	SA	VP	0.01	0.1			0.8	0.1	0.1		1.1	0.03						
<i>Carex panicea</i>	?	VE										0.03						
<i>Carex rupestris</i>	SR	VE						0.01										
<i>Carex vaginata</i>	SR	VE	0.02							0.1								
<i>Deschampsia flexuosa</i>	SA	VE	1.8	1.1	0.1	0.3	0.01	0.01	0.1	10.3	0.3		0.01	0.2				0.02
<i>Festuca ovina</i>	SA	VP	0.2	0.2		0.5	0.03		0.1	0.3	0.2	1.0	0.9		0.01	2.2	0.04	
<i>Festuca vivipara</i>	NS	VE											0.1					
<i>Hierochloa alpina</i>	?	VP															0.04	
<i>Juncus trifidus</i>	SA	VI	0.01	0.2	0.1	0.2		0.01	0.5		0.3	0.4	0.6	0.1			0.4	0.02
<i>Luzula</i> sp.	SA		0.01										0.01					0.1
<i>Luzula arcuata</i>	SA	VI			0.01		0.8	0.5					0.01				0.1	0.3
<i>Luzula multiflora</i>	SA	VP		0.1						0.01	0.01		0.01		0.01			
<i>Luzula spicata</i>	SA	VP		0.01		0.1		0.1	0.2		0.1	0.2	0.2					
<i>Phleum alpinum</i>	SA	VP		0.1						0.01								
<i>Poa alpina</i>	SA	NV	0.04	0.4		0.1												
<i>Trisetum spicatum</i>	SA	VP					0.1	0.2	0.03	0.01								
<i>Vahlodea atropurpurea</i>	SA	VP					0.1		0.1		0.01							

Appendix 2. The densities m^{-2} of 0- to 3-year-old seedlings in 15 plant communities in the summers of 1995–1996. NV = no vegetative reproduction, VP = vegetative reproduction is possible, VI = vegetative reproduction is ineffective, VE = vegetative reproduction is effective. R.G. = regenerative group.

Species	R.G.	Plant community														
		EUBED	EUME	SAL	TALU	RANU	OXY	PATT	TALL	GRBED	GRHE	TREMP	MYRT	CASS	TRCASS	EMP
Dwarf shrubs																
<i>Betula nana</i>	VE												0.4			
<i>Cassiope hypnoides</i>	VE							0.4								
<i>Cassiope tetragona</i>	VP						0.1	9.6						2.0		
<i>Empetrum nigrum</i>	VE		0.3							1.6		0.7	3.8	4.0		
<i>Phyllodoce caerulea</i>	VP							4.0		0.7			1.2	0.5		
<i>Vaccinium myrtillus</i>	VE		0.1													
<i>Vaccinium vitis-idaea</i>	VE										0.3					
Herbs																
<i>Alchemilla</i> sp.	VI		0.5								0.2					
<i>Antennaria</i> sp.	VE		1.0										0.1			
<i>Astragalus alpinus</i>	VI		0.1								0.7					
<i>Campanula rotundifolia</i>	VE				2.1						7.9					
<i>Cardamine bellidifolia</i>	NV	0.3			0.4	8.7	9.4			0.3					0.1	
<i>Cerastium</i> sp.	VP	0.5	0.3		80.7		10.0			1.3					0.1	
<i>Euphrasia frigida</i>	NV		20.8							0.4						
<i>Geranium sylvaticum</i>	NV									0.7						
<i>Gnaphalium supinum</i>	VI	72.0	11.4	181.0	50.8	3.0	7.2	3.9		0.3	0.8	0.1				
<i>Hieracium</i> sp.	NV		0.8	0.7	2.9						0.1					
<i>Hieracium alpina</i>	NV				1.4			0.5		1.4						
<i>Minuartia biflora</i>	NV				1.2						0.3	0.1				
<i>Oxyria digyna</i>	VP				1.8	19.0	6.5									
<i>Potentilla crantzii</i>	VP		1.2								0.7					
<i>Pyrola</i> sp.	VE		0.2													
<i>Ranunculus</i> sp.			9.5													
<i>Ranunculus acris</i>	VP	1.4	0.4								13.5					
<i>Ranunculus glacialis</i>	NV					42.0	0.5									
<i>Ranunculus nivalis</i>	NV		1.8													
<i>Ranunculus pygmaeus</i>	NV					5.6	2.6									
<i>Rumex acetosa</i>	NV									0.7						
<i>Saussurea alpina</i>	VE	0.1	0.9							0.8						
<i>Sibbaldia procumbens</i>	VP	18.6	46.0	15.0	1.4	3.3	0.8	0.7			0.8					
<i>Silene acaulis</i>	NV							0.8								
<i>Solidago virgaurea</i>	VP		1.2	0.3												
<i>Taraxacum</i> sp.	NV	18.1	9.2		1.6	0.1										
<i>Tofieldia pusilla</i>	VP							10.8								
<i>Trollius europaeus</i>	NV									1.6						
<i>Veronica alpina</i>	VU	76.2	22.1		11.8		1.3	0.5								
<i>Viola biflora</i>	NV	24.3	77.2		2.7					4.8						
Grasses and sedges																
<i>Agrostis mertensii</i>	VP		2.1	0.3				0.4		2.1						
<i>Anthoxanthum odoratum</i>	VI	0.3	13.7	1.7	3.8			0.4	0.1							
<i>Carex</i> sp.			0.3	0.3								0.4				
<i>Carex bigelowii</i>	VE		0.1							0.8					0.4	
<i>Carex lachenalii</i>	VP			0.3		3.6	0.3			6.8						

Continued

Appendix 2. Continued.

Species	R.G.	Plant community															
		EUBED	EUME	SAL	TALU	RANU	OXY	PATT	TALL	GRBED	GRHE	TREMP	MYRT	CASS	TFCASS	EMP	
<i>Deschampsia flexuosa</i>	VE	0.3	0.9		0.1								0.4				0.1
<i>Festuca ovina</i>	VP		0.3		2.5	0.1		0.4		0.3		3.1		0.4	0.1		
<i>Juncus</i> sp.	VI				0.3												
<i>Juncus trifidus</i>	VI										0.1	2.7					
<i>Luzula</i> sp.	VP	0.4	0.4	0.4	1.8	25.0	2.2	2.5		1.0	12.0	2.8		3.1	4.2		
<i>Trisetum spicatum</i>	VP			0.1		0.7	1.6	1.3									
<i>Vahlodea atropurpurea</i>	VP					0.7											
UNID					2.3	0.1		0.3					1.0	0.7	0.1		