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Characteristics of the seedling flora in alpine vegetation, subarctic Finland, I. Seedling densities in 15 plant communities

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Samples of mature vegetation and seedling flora were taken in 15 plant communities at Kilpisjärvi, subarctic Finland. The first aim of the study was to investigate seedling densities in different plant communities. The second, was to explore the importance of different regenerative groups, severe disturbances, altitude as well as cover of vegetation, bryophytes and litter in the prediction of seedling densities. Contrary to a common prediction, seedlings were abundant in many plant communities. The mean seedling density was closely related to the cover of the regenerative groups in the mature vegetation types and not related to the environmental factors. The densities did not decrease with altitude. Severe disturbances did not usually lead to higher seedling density, either. Thus estimating the cover of the regenerative groups in mature vegetation is a most useful tool in the prediction of seedling densities. By exploring the cover of the regenerative groups it is possible to map the landscape in terms of the seed regeneration for the purpose of restoration plans.

Keywords: alpine vegetation, ecological restoration, regenerative groups, seedling density, severe disturbances

INTRODUCTION

The ecological significance of reproduction by seed in arctic and alpine areas is undergoing reassessment (Urbanska & Schütz 1986, McGraw & Vavrek 1989, McGraw & Fetcher 1992, Chambers 1993). Even nowadays it is often assumed that seedling recruitment is of minor significance in determining regeneration of populations (Archibold 1995). Vegetative reproduction is assumed to be the dominant regenerative strategy (Bliss 1971, Billings 1974, Archibold 1984, 1995), because recruitment by seed is episodic and unpredictable in these harsh environments. In arctic and alpine areas, flowering, seed production and seed germination often fail (Billings 1974), seedlings are not common (Bliss 1971) and seedling survival rates are low (Wager 1938, Billings 1974). Furthermore, the importance of seed regeneration has been assumed to be less important in higher altitudes of montaneous areas than in lower altitudes (Montalvo *et al.* 1991). However, in many arctic and alpine plant communities seedling densities may be several hundreds, even thousands per m^{-2} (Söyrinki 1938, McGraw & Shaver 1982, Freedman *et al.* 1982). Few empirical studies have been carried out to test the correlation between altitude and the seed regeneration ability of communities.

It is often assumed that seedling densities are lower in the high than in the low altitudes, because the high altitudes are more harsh and risky to germination and seedling recruitment than the low altitudes (Bruggink 1993 cit. in Vera 1997, Maruta 1983, 1994). Furthermore, litter (Facelli *et al.* 1992), mosses (van Tooren 1990) and established plants (Fenner 1985) prevent seedling recruitment. Disturbances improve nutrient and temperature conditions thus providing safe-sites for germination and seedling recruitment (e.g. Amen & Bonde 1964, Reynolds 1984, Haggas *et al.* 1987, Chambers *et al.* 1991, Chambers 1995).

First we studied seedling densities of different plant communities at Kilpisjärvi, in Finnish Lapland. Next we set out to find the most useful factor in the prediction of the communities' ability for seed regeneration. This information has applications in mapping the landscape in terms of seed regeneration ability for ecological restoration. For this purpose we analysed relationships between the seedling densities and the cover of regenerative groups, altitude, vegetation, bryophytes, bare ground and litter. We assumed that in this extensive scale the cover of the regenerative groups should be the most important among the influential factors. We went on to study the effects of severe disturbances on seedling densities. We predicted that the densities should be higher in severely disturbed plant communities than in their relatively undisturbed counterparts. As far as we know, only one study concerning the seedling densities among plant communities in the alpine areas has been published (Söyrinki 1938).

MATERIAL AND METHODS

Abbreviations and nomenclature

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-Gymnomitrion* snowbed, PATT = patterned ground, RANU = *Ranunculus glacialis-Gymnomitrion* 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 in the summers of 1995–1996. The altitudes of the study sites varied from 570 m to 950 m (Table 1). For this reason 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. The last group consisted of two heaths trampled by humans (TREMP and TRCASS), a patterned ground broken by thawing and freezing processes (PATT) and a herb-rich talus slope (TALU) disturbed by moving gravels. These severely disturbed plant communities have relatively undis-

Table 1. The plant communities of the study sites in the summers of 1995-1996. The abbreviations of the plant communities: 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-Gymnomitrion* snowbed, PATT = patterned ground, RANU = *Ranunculus glacialis-Gymnomitrion* 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. Other abbreviations: B = bare ground, Br = bryophytes, C% = cover, COMM = plant community, D = dwarf shrubs, E = elevation above sea level, Gs = grass-like species, H = herbs, L = litter, Li = lichens, R = rockiness, V = vegetation.

COMM	E m	V C%	B	L	R	D	Gs	H	Br	Li	Dominant taxa in the ground layer	Dominant taxa in the field layer	Disturbance factor
MYRT	600	86.7	2.0	25.0	1.6	20.0	0.4	0.2	64.2	7.2	*Dicranum* sp. (57.5%), *Lophozia* sp. (5.0%)	*Empetrum nigrum* (10.9%), *Vaccinium myrtillus* (3.4%)	Reindeer grazing, tracks, low intensity
EMP	650	89.6	0.0	24.6	0.6	41.7	2.7	0.08	77.1	2.6	*Pleurozium* sp. (35.6%), *Hylocomium* sp. (23.3%)	*Empetrum nigrum* (32.9%), *Betula nana* (7.4%)	Reindeer tracks, low intensity
CASS	900	87.5	6.4	7.0	2.9	24.6	1.9	0.01	69.2	13.1	*Dicranum* sp. (66.7%), *Barbilophozia* sp. (66.7%)	*Empetrum nigrum* (8.5%), *Cassiope tetragona* (12.4%)	Reindeer grazing, low intensity
GRHE	850	46.7	5.0	47.1	7.4	3.3	4.4	1.3	20.4	14.5	*Dicranum* sp. (14.3%), Crustaceous lichens (11.2%)	*Carex bigelowii* (2.9%), *Cassiope hypnoides* (1.9%)	Reindeer grazing, tracks, low intensity
GRBED	800	87.1	7.2	15.2	3.1	5.3	6.3	0.6	69.2	13.9	*Dicranum* sp. (37.8%), *Barbilophozia* sp. (11.7%)	*Carex bigelowii* (3.9%), *Phyllodoce caerulea* (2.3%)	Thawing and freezing processes, low intensity
EUBED	820	65.0	9.7	35.8	7.4	4.4	11.2	13.0	54.2	0.9	*Sanionia* sp. (14.8%), *Dicranum* sp. (14.3%)	*Viola biflora* (5.3%), *Carex bigelowii* (3.6%)	Reindeer grazing, channels of melting water, low intensity
RANU	845	57.5	4.8	3.5	33.8	14.2	1.8	3.1	40.9	3.9	*Gymnomitrion* sp. (14.7%), *Lophozia* sp. (11.7%)	*Cassiope hypnoides* (13.6%), *Ranunculus glacialis* (1.5%)	Thawing and freezing processes, low intensity
OXY	820	39.6	12.9	3.3	43.3	0.9	0.9	3.2	39.6	3.0	*Gymnomitrion* sp. (22.5%), *Barbilophozia* sp. (11.8%)	*Oxyria digyna* (1.6%)	Thawing and freezing processes, low intensity
SAL	800	57.5	13.8	6.5	23.2	12.8	1.4	3.6	36.7	5.5	*Lophozia* sp. (14.3%), *Dicranum* sp. (6.2%)	*Cassiope hypnoides* (9.6%), *Salix herbacea* (3.7%)	Thawing and freezing processes, low intensity
TALL	560	42.5	0.0	86.7	9.4	1.8	16.7	26.7	8.7	0.03	*Pleurozium* sp. (5.6%), *Barbilophozia* sp. (1.3%)	*Trollius europaeus* (6.7%), *Geranium sylvaticum* (4.7%)	Reindeer grazing, low intensity
EUME	570	56.7	1.6	45.0	8.9	1.1	5.7	9.9	37.5	0.6	*Polytrichum* sp. (9.8%), *Sanionia* sp. (9.8%)	*Viola biflora* (5.2%), *Carex bigelowii* (2.3%)	Reindeer grazing, tracks, low intensity
TREMP	650	13.3	62.9	23.9	11.8	9.4	2.8	0.03	1.6	0.2	*Polytrichum* sp.(1.1%)	*Empetrum nigrum* (6.7%), *Carex bigelowii* (1.0%)	Human trampling, severe intensity
TRCASS	950	19.6	41.7	4.3	45.6	5.8	2.9	0.00	10.3	1.7	*Dicranum* sp. (5.1%), *Pohlia* sp. (1.4%)	*Betula nana* (2.8%) *Festuca ovina* (2.2%)	Human trampling, severe intensity
PATT	800	47.5	33.1	5.8	14.1	7.8	2.5	1.5	36.7	9.8	*Barbilophozia* sp. (16.6%), *Polytrichum* sp. (6.2%)	*Phyllodoce caerulea* (3.1%), *Salix herbacea* (2.2%)	Thawing and freezing processes, severe intensity
TALU	570	7.4	52.9	1.5	47.1	0.1	2.2	4.3	0.5	0.1	*Lophozia* sp. (0.04%), *Bryum* sp. (0.04%)	*Taraxacum* sp. (1.0%), *Campanula rotundifolia* (0.8%)	Falling gravel, reindeer trampling, severe intensity

turbed counterparts: EMP, CASS, GRBED and EUME, respectively. Other plant communities were also affected by disturbances, but their intensity was low.

At almost all sites, bryophytes were the dominant group of plants (Table 1). On heaths, PATT, GRBED, EUBED and EUME, the bryophyte cover consisted of mosses (*Pleurozium schreberi, Dicranum* sp. and *Hylocomium splendens* on heaths and GRBED and *Sanionia uncinata* at EUBED and EUME). At the snowbed sites where snow remains for a prolonged period (RANU, OXY and SAL) and at PATT, the ground layers were dominated by hepatics (e.g. *Lophozia* sp., *Gymnomitrion* sp. and *Barbilophozia* sp.).

The field layers of MYRT, EMP, TREMP, CASS, TRCASS, GRHE, PATT and GRBED were dominated by dwarf shrubs and grass-like species. RANU and SAL were dominated by trailing dwarf shrubs and herbs. Grass-like species and herbs dominated at EUBED, TALL, EUME and TALU. At OXY herbs were the dominants.

Sampling

At the 15 study sites, three parallel 7-m-long transects were established three metres from each other. Along each transect, four 80 cm × 80 cm squares (Oksanen & Virtanen 1995) were placed systematically one metre from each other. Thus, 12 squares were studied at each site and there were 180 squares in all.

Cover values of vascular plant species and genera of lichens and bryophytes and their growth forms (dwarf shrubs, herbs, grass-like species, lichens and bryophytes) were recorded visually, in addition to the cover values for vegetation, bare ground, litter and rocks based on a cover scale of one of the following values: 0.1%, 0.5%, 1%, 2%, 3%, 5 %, 7%, 10%, 15%, 20%, 30%, ..., 80%, 90%, 95%, 100%. 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 we used the system described by Söyrinki (1938). He divided alpine species into four groups regarding their different abilities to reproduce vegetatively. These groups in turn were divided into three subgroups characterized by different patterns of seedling production. The main groups were: NV = no vegetative reproduction, NP = little, if any, vegetative reproduction, VI = vegetative reproduction being ineffective at maintaining populations, and VE = vegetative reproduction being effective at maintaining populations. The sub-groups were (A) no seedlings found, (B) seedlings infrequent, and (C) seedlings frequent. Most species of subgroup C belonged to the main groups NV, NP and VI. All three sub-groups were well represented in group VE, although sub-group A is dominant.

Statistics

Statistical analyses were carried with SPSS Release 7.5. Non-parametric tests were applied in the analysis of the seedling densities because of non-normal distributions. The variation of the seedling densities among the 11 sites was first analysed with the Kruskal-Wallis test, and then a test for non-parametric multiple comparisons based on the Mann-Whitney statistics was applied (Sokal & Rohlf 1995). The seedling densities of the relatively undisturbed and the severely disturbed plant communities were compared with the Mann-Whitney test. We used the Spearman's rank correlation analysis in testing the relationships between the seedling densities and altitude as well as between the seedling densities and the cover of different regenerative groups, bare ground, mature vegetation and bryophytes. The cover of the different regenerative groups were calculated by adding the cover estimates of the species.

RESULTS

The variation in the seedling density among the 11 sites was very high ($H = 109.2$ based on the Kruskal-Wallis-statistics, $p < 0.001$): the density ranged from 0.2 to 226.7 seedlings m^{-2} (Fig. 1). The density was lower in the plant communities dominated by dwarf shrubs and grass-like species (0.2–15.2 seedlings m^{-2}) than in the plant communities dominated by trailing dwarf shrubs and herbs (111–200 seedlings m^{-2}) and in the plant communities dominated by herbs and grass-like species (32.9–226.7 seedlings m^{-2}).

The cover values of the species with effective vegetative reproduction were highest on the heaths, RANU and SAL and lowest at OXY, EUME and TALU (Table 2). The plants which do not reproduce vegetatively were almost completely absent on the dwarf shrub heaths. Their relative cover values were greatest at EUBED, meadows and TALU. There was a positive correlation between the seedling densities and the plants with no vegetative reproduction ($p < 0.01$) and those with ineffective vegetative reproduction ($p < 0.01$, Table 3). There was a negative correlation between the seedling densities and the cover values ($p < 0.01$) of the group that showed effective vegetative reproduction. The seedling densities were not higher in the low altitudes than in the high altitudes. There was no correlation between the densities and the tested environmental factors. In most cases there was no statistically significant difference in the seedling density between the severely disturbed plant communities (TREMP, TRCASS, PATT, TALU) and their relatively undisturbed counterparts (EMP, CASS, GRBED, EUME, Fig. 2).

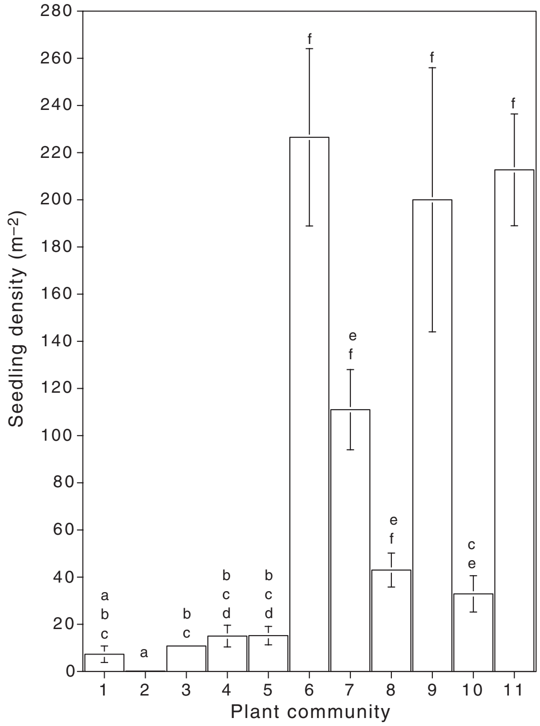

Fig. 1. The mean seedling densities (seedlings m^{-2}) in 11 alpine plant communities. The same letters indicate that there is no statistical difference between the compared seedling floras. 1 = *Vaccinium myrtillus-Dicranum* heath, 2 = *Empetrum nigrum-Pleurozium schreberi* heath, 3 = *Cassiope tetragona-Empetrum nigrum-Dicranum* heath, 4 = siliceous grass and sedge heath, 5 = siliceous grass and sedge snowbed, 6 = eutrophic low herb snowbed, 7 = *Ranunculus glacialis-Gymnomitrion* snowbed, 8 = *Oxyria digyna-Gymnomitrion* snowbed, 9 = *Salix herbacea-Cassiope hypnoides* snowbed, 10 = *Trollius euoropaeus-Geranium sylvaticum* tall herb meadow, 11 = eutrophic low herb meadow. Non-parametric multiple comparisons based on the Mann-Whitney statistics was used; $n = 12$. $p > 0.05$. SE-values are presented.

DISCUSSION

Seedlings were abundant in many plant communities. This result challenges the earlier widely accepted views (Bliss 1971, Billings 1974, Bell & Bliss 1980, Archibold 1995). The pattern in the mean seedling densities is similar to the pattern in the seedling densities in the Petsamo District (Söyrinki 1938): the values are higher in the meadows and the snowbeds than on the heaths. As predicted, this observed pattern of the seedling density is closely related to the cover values of the regenerative groups. The high cover of the species with effective vegetative reproduction leads to low means of the seedling densities. The high cover of the species with an inability for vegetative reproduction or those with an ineffective vegetative reproduction ability leads to the high seedling densities.

Why didn't the moss and litter covers have any statistically significant effects on the seedling densities? The reasons for this may be both variable

Table 2. Cover (%) of the regenerative groups. NV = no vegetative reproduction, VP = vegetative reproduction possible, VI = vegetative reproduction ineffective, VE = vegetative reproduction effective. C% = cover of the species in the different vegetative groups as a percentage of the total cover of all species. The system of regenerative groups after Söyrinki (1938) was used. X = regenerative group absent from the plant community.

Plant community	NV C%	VP C%	VI C%	VE C%
Vaccinium myrtillus-Dicranum heath	X	13.3	0.2	86.7
Empetrum nigrum-Pleurozium schreberi heath	X	1.2	0.1	99.1
Cassiope tetragona-Empetrum nigrum heath	X	41.8	0.4	58.0
Siliceous grass and sedge-heath	2.2	14.3	4.0	79.5
Siliceous grass and sedge snowbed	4.1	32.1	2.8	61.1
Eutrophic low herb snowbed	27.3	14.1	18.9	39.9
Ranunculus glacialis-Gymnomitrion snowbed	7.7	13.4	4.7	74.2
Oxyria digyna-Gymnomitrion snowbed	9.9	55.0	15.4	19.8
Salix herbacea-Cassiope hypnoides snowbed	0.1	5.7	14.8	79.4
Trollius europaeus-Geranium sylvaticum tall herb meadow	31.5	19.7	7.6	41.0
Eutrophic low herb meadow	39.4	11.5	13.9	35.2
Trampled *Empetrum nigrum* heath	0.2	9.3	4.6	85.8
Trampled *Cassiope tetragona* heath	X	32.6	7.8	59.5
Patterned ground with low grasses and sedges	7.2	45.0	5.4	42.4
Slightly calcareous low herb talus slope	31.4	22.9	19.8	26.3

Table 3. The correlation between the seedling densities and the mean cover of the regenerative groups, the seedling densities and the mean cover of vegetation, mosses and litter as well as the seedling densities and the altitude. The Spearman's rank correlation analysis was applied. ** = $p < 0.01$, $n = 15$. NV = no vegetative reproduction, VP = vegetative reproduction possible, VI = vegetative reproduction ineffective, VE = vegetative reproduction effective.

Variables	Seedling density
NV	0.72**
VP	0.01ns
VI	0.80**
VE	–0.65**
Bare ground	0.10 ns
Vegetation	–0.14 ns
Bryophytes	–0.16 ns
Litter	0.10 ns
Altitude	0.22 ns

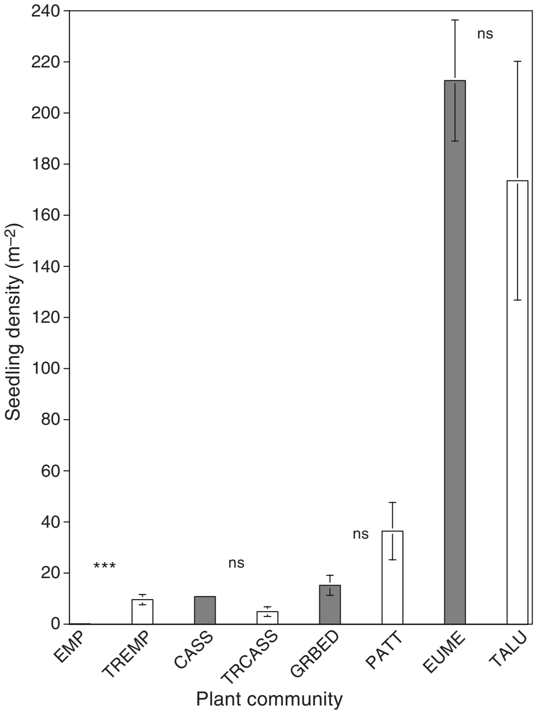

Fig. 2. The comparison of the seedling densities in severely disturbed and relatively undisturbed plant communities. CASS = *Cassiope tetragona-Empetrum nigrum-Dicranum* heath, EMP = *Empetrum nigrum-Pleurozium schreberi* heath, EUME = eutrophic low herb meadow, GRBED = siliceous low grass and sedge snowbed, PATT = patterned ground, TALU = slightly calcareous low herb talus slope, TRCASS = trampled *Cassiope tetragona* heath, TREMP = trampled *Empetrum nigrum* heath. Non-parametric multiple comparisons based on the non-parametric Mann-Whitney test was used; $n = 12$. *** = $p < 0.001$, ns = not significant. SE-values are presented. Grey bars = relatively undisturbed communities, white bars = severely disturbed communities.

thickness of the litter and the moss taxa between the communities and the variation in the safe-site requirements of the vascular plant species.

The fact that seedling densities lack a positive correlation with an altitude is a similar result to the pattern of seed bank densities in Québec (Morin & Payette 1988). The seedling densities are lower in low altitudes, where the area of meadows and snowbeds is smaller in comparison to high altitudes.

The seedling densities of the severely disturbed plant communities were usually not higher than those of their relatively undisturbed counterparts. This was an unexpected result. Probable reasons for this are the continuity of disturbances as well as compactness or mobility of soil at the disturbed sites, which prevents seed entrapment and seedling recruitment.

In summary, we conclude that the estimation of the cover of the regenerative groups is a most useful tool in the prediction of the seedling densities of the communities. By knowing the cover it is possible to construct seed regeneration-maps for the purpose of ecological restoration.

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