

Herb abundance and life-history traits in two contrasting alpine habitats in southern Norway

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Received 5 November 2003; accepted in revised form 30 December 2004

Key words: Clonality, Oceanic, pH, Recruitment, Seed weight, Sub-continental

Abstract

Colonisation is often a critical stage in the life history of plants, and recruitment success is expected to have a strong impact on plant frequencies especially among herbs. Several plant traits (seed size, plant height, leaf dry weight and specific leaf area) are suggested to be functionally important in early life stages, and the impact of such traits is expected to increase with habitat harshness. In this comparative study we examine the relative role of different plant traits for herb community patterns on both a local and regional scale in two contrasting alpine ecosystems in southern Norway: (1) a sub-continental region with more dry and productive, base-rich soils (Ho1, Hallingdal) and (2) an oceanic region, with humid acidic soils (Setesdal). Differences in species richness between regions were mainly due to higher herb richness in the base-rich region ($n=55$) than in the acidic region ($n=13$). Among traits, herb species seed weight was higher at the acidic site. The relative importance of traits for explaining herb local abundance and regional distribution tended to be stronger at the acidic site. No trait had a significant effect at the base-rich site, although seed weight and seed number were marginally non-significant. Plant clonality was positively related to local abundance and marginally to regional distribution at the acidic site. Plant frequency-trait correlations were generally higher in the acidic region than in the base-rich region. There was further a (marginal) increase of herbs with large seeds and with a dependence on sexual reproduction with increasing pH levels in Ho1. Soil pH was also the most important environmental variable for herb richness in Ho1, while no environmental variable was significantly related to herb richness in Setesdal. The study suggests that recruitment through seed is critical for the alpine herb community patterns especially in harsh habitats. Possible explanations for recruitment constraints include both soil acidity (low pH and Ca levels in addition to possible aluminium toxicity) and disturbance through grazing.

Introduction

The identification of plant traits with functional importance for plant community dynamics has been a central ecological issue in recent years

(McIntyre et al. 1999; Lavorel and Garnier 2002). Several studies have focused on traits important for colonisation and establishment such as seed size, plant height, leaf dry weight and specific leaf area (cf. Weiher et al. 1999). Seed size has been

identified as a key functional trait with respect to colonisation (Eriksson and Jakobsson 1998; Moles and Westoby 2002). Other studies fail to find any clear relationship between functional traits and plant frequency, and Leishman (1999) suggests that a plant's ability to establish is context dependent. In general, traits are expected to have a stronger relationship with plant frequencies in harsh habitats (Grime 1979; Westoby et al. 1997; Reader 1998; Bullock 2000). This is in accordance with a more general ecology hypothesis stating that high species richness is related to a relaxation of niche structuring forces in habitats with a low stress level (Hubbell 2001). Hence, selection for specific life history traits exerted by harsh environments should result in a strong relationship between trait distribution and plant community patterns in habitats such as alpine plant communities.

Although the number of viable plant life histories in alpine habitats is limited, the environment is known to be extremely heterogeneous with large ranges in both plant traits and frequency values along gradients (Körner 1999). Biodiversity "hotspots" in Norwegian mountains are found in regions with narrow tolerances for July and January temperatures at calcareous bedrock (Birks 1996; Sætersdal and Birks 1997), and alpine plant species richness was positively correlated with base-richness at local scales (Austrheim et al. 1999). Gough et al. (2000) found soil pH to be the best predictor for species richness both at the regional and the local scale in North-American arctic tundra. High species richness at non-acidic sites was correlated with the occurrence of herbs with relatively short life cycles and with a high dependence on seed reproduction (i.e. non-clonal species) (Gough et al. 2000). This suggests an interaction between pH and plant traits such as reproduction strategy. A recent study has also shown restricted recruitment by seed at low pH (Roem et al. 2002). Although the herb species pool includes several strictly clonal species, seed recruitment is considered to be of superior importance for herb species as compared to woody species and graminoids that in general are clonal (except within coniferous plants). Hence, one could expect traits affecting colonisation ability to be related to herb frequencies (cf. Westoby 1998; Weiher et al. 1999) especially if the herbs are non-clonal.

Few empirical studies are available on the importance of plant traits for plant colonisation in alpine habitats, or how this may interact with key environmental factors such as soil pH. Seed weight was positively related to herb survivorship on barren heath in subalpine habitats (Wood and Del Moral 1987). Moreover, plant traits were found to be important for explaining differential recruitment patterns of herbs in contrasting subalpine grassland habitats (Austrheim and Eriksson 2003). Low-stature plants with low specific leaf area and low leaf dry-weight had higher recruitment in habitats exposed to drought; i.e. recruitment could be predicted by plant traits in the dry grasslands only. Clonality is a common strategy in stressful habitats (de Kroon and van Groenendael 1997). This ability for vegetative reproduction is often species specific, and the relative importance of vegetative versus reproduction through seed has been found to differ among alpine habitats (Wood and Del Moral 1987; Chambers 1995; Welling and Laine 2000). Differences are related to e.g. nutrient status, soil properties, disturbance and temporal climatic variability (Chambers 1995). Both the total number of plant species dependent on seed production, and the relative frequencies of seed reproducing plants should be higher in productive than in less productive alpine habitats (cf. Welling and Laine 2000).

In this study, we present new data on how herb functional plant traits including seed weight, seed number, plant height, leaf dry-weight, specific leaf area and clonality are related to local abundance and regional distribution patterns in a sub-continental alpine region with more dry and base-rich soils (Ho1, Hallingdal) and an oceanic alpine region with humid acidic soils (Setesdal). The following predictions are addressed: (1) Species richness (both local and regional) is expected to be higher in the non-acidic alpine habitat (Ho1) as compared to the acidic habitat (Setesdal), due to a higher herb richness in the non-acidic habitat. (2) We predict a higher mean seed weight for herbs in the low productive habitat (Setesdal), while leaf dry weight (LDW), specific leaf area (SLA), seed number, plant height (PLH) and the number of strictly sexually reproducing herb species are expected to be higher in the non-acidic habitat (Ho1). (3) Herb frequencies are expected to increase with seed weight and decrease with seed numbers. We predict a negative correlation

between herb frequency and each of: (4) SLA, (5) LDW and (6) PLH, respectively. (7) Plant traits are expected to be better predictors of plant frequency variation in the harsh (acidic) habitat (“traits matter”) than in the base-rich habitat (“traits do not matter”), due to more favourable conditions for plant colonisation in the latter. (8) We expect plant frequency-trait relationships to be affected by the environment, and predict that the occurrence of herbs depending on sexual reproduction increases with pH within regions.

Material and methods

Study sites

Setesdal, Vest-Agder and Aust-Agder, SW Norway (58°59' N, 6°58' E) has an oceanic alpine climate with high annual precipitation (between 1170 and 1760 mm as recorded at the closest weather stations, Førland (1993)). The bedrock is Precambrian granite, which is resistant to weathering and gives rise to acidic mineral soils poor in nutrients (Holtedahl 1969). Ho1, Buskerud, S Norway (60°40' N, 7°55' E) has a sub-continental alpine climate with moderate to low annual precipitation (700–800 mm, Førland 1993). The bedrock consists of meta-arkose (Sigmond 1998), which gives rise to moderately base-rich soils, especially in landscape depressions with seepage water. Both sites are grazed by sheep (50 per km² in Setesdal and <10 per km² in Ho1 in 2000) and reindeer (<0.5 per km² in both regions in 2000).

Plant community and environmental data

Vascular plant community and soil environmental data were sampled in the low alpine region (cf. Moen 1998) in 2000 (Setesdal) and 2001 (Ho1). In each region, 0.25 m² plots were placed in southerly exposed slopes spanning the topography-snow cover gradient from ridge, via lee-side to moderate and late snow patches. Peatland habitats and plots with more than 10% cover of bedrock and stones were excluded at both sites. The Ho1 study area, 181 plots were randomly chosen within an area of approximately 2.7 km² but with a balanced stratified distribution among

habitats and altitudinal levels (ca. 1100–1300 m.a.s.l.). In Setesdal, plots were sampled at 10 different sub-sites (each 0.2 ha) with a balanced stratified distribution within an area of 124 km² at ca. 900–1000 m a.s.l. Twenty plots (0.25 m² each) were placed randomly at each sub-site (200 plots in total). Plant species frequency in each plot is based on presence-absence within 16 subplots (0.0156 m²). The frequencies are expressed at both a local and a regional scale. Local abundance denotes mean frequency in all plots where the species occur. Regional distribution denotes the percentage of plots where the species is present in relation to the total number of plots within each region.

Soil environmental data include pH, loss on ignition (LOI), dry matter (DM), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na). All soil analyses follow international standards (Krogstad 1992) and were performed at Norwegian Centre for Soil and Environmental Research (Jordforsk) except for LOI and DM which were performed at Department of Biology, University of Oslo.

Plant traits

Data on plant traits were sampled from plant specimens collected at the seed dispersal stage ($n=10$). These include: (1) seed weight (SW) measured as mean weight after drying in ca. 3 weeks at ca. 20 °C; (2) plant height (PLH), i.e. the absolute height independent of leaf height; (3) leaf dry weight (LDW) measured as mean dry weight of the largest fully expanded leaf (mg); (4) specific leaf area (SLA) which is the mean leaf area/dry weight (mm²/mg), and (5) number of seeds per plant. Data on the species ability for vegetative reproduction (i.e. clonality) was compiled mainly from the literature (Söyrinki 1938; Grime et al. 1988; Eriksson and Jakobsson 1998, Dupre and Ehrlen 2002, Austrheim unpubl.). All species and life history traits are presented in Appendix 1.

Statistical analyses

We used linear regression to analyse the relationship between plant frequencies at local and

regional scale and continuous plant traits (i.e. plant height, seed number, seed weight, LDW, SLA and clonality). All species frequency values were arcsine transformed, while plant trait values (except for clonality) were In-transformed prior to the analysis to stabilise the variance. Each region was treated separately since several species occurred in both regions. In comparative analysis, all species cannot be regarded as full replicates, due to common ancestry. We therefore tested for possible phylogenetic effects by calculating a set of phylogenetically independent contrasts in each plant community Harvey and Pagel 1991) using the program COMPARE (Martins 2003). The phylogenetic tree is based on recent angiosperm phylogenies (Angiosperm Phylogeny Group 1998), and relations within families are based on Bremer (1994; Asteraceae); Olmstead et al. (2001; Scrophulariaceae) and Eriksson et al. (2003; Rosaceae).

We examined the relationship between soil environmental variation and herb richness using a stepwise generalised linear model (GLM) with a Poisson error distribution for the response variable and backward eliminations of explanatory variables. Soil variables (LOI, DM, P, K, Ca, Mg and Na) were In-transformed prior to the analysis. Secondly, we examined if plant frequency–plant trait relationships were affected by important environmental variables. This analysis was however difficult, since several species have a unimodal distribution along environmental gradients (Økland 1990). We included soil pH which fitted a linear (or close to linear) model, and included all species with a frequency >5% that were significantly related to pH. However, most species were absent from the majority of plots. Hence, plant frequencies showed a binomial distribution and was transformed to presence–absence data in each plot and then analysed by logistic regression. The resulting slope estimates (β -pH values) were

further used to analyse the importance of pH for herb traits–frequency relations in a linear model with trait values as explanatory variables. Analyses were performed in S-Plus vs. 6.1. when no other software is specified.

Results

Main differences in species composition, soil and herb traits between regions

Striking differences in vascular plant species richness between regions were observed both at the regional and the local scale ($t = -7.06$, $p < 0.0001$). The acidic region (Setesdal) comprised 50 species and 8.0 ± 1.0 (mean \pm S.D.) species at the small scale. The base-rich region (Ho1) comprised 104 species, while 12.2 ± 7.2 species were found at the small scale. Differences in vascular plant richness among regions were mainly related to a higher herb species pool at the base-rich site, which comprised 55 herb species (53% of all vascular plants recorded at the site) as compared to 13 herb species (26%) at the acidic site. Ten herbs were found at both sites. Only 4 species occurred exclusively at the acidic site; two strictly oceanic species (*Narthecium ossifragum* and *Cornus suecica*), while the other two (*Gentiana pupurea* and *Trifolium repens*) also occurred at the base-rich site, outside plots.

Soil samples showed a higher pH level in Ho1 (4.45 ± 0.03 , mean \pm SE) as compared to Setesdal (4.41 ± 0.02), but differences were surprisingly low and not significant. Calcium (which correlated positively and negatively with pH in Ho1 and Setesdal, respectively; Austrheim et al. in press) was significantly higher in Ho1 (mean 49.10 ± 3.88 mg/100 g) as compared to Setesdal (36.1 ± 2.10 mg/100 g). Ho1 samples also had significantly lower soil moisture level (measured

Table 1. Soil variables (mean \pm SE) measured for Setesdal ($n = 200$) and Ho1 ($n = 181$).

	P (mg/100 g)	K (mg/100 g)	Ca (mg/100 g)	Mg (mg/100 g)	Na (mg/100 g)	pH	DM (%, g/100 g)	LOI (%, g/100 g)
Setesdal	13.68*** ± 0.41	42.50*** ± 1.14	36.07 ± 2.10	21.21*** ± 0.97	6.73*** ± 0.24	4.41 ± 0.02	30.36 ± 1.08	70.35*** ± 1.97
Ho1	6.05 ± 0.27	13.81 ± 0.79	49.10** ± 3.88	8.45 ± 0.43	2.48 ± 0.11	4.45 ± 0.03	62.37*** ± 1.28	20.49 ± 1.43

Bold values denote significant differences between regions (two-sample t -test). * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

as dry matter levels and loss on ignition) than in the Setesdal samples.

Plant traits differed between herb species in the two contrasting regions as predicted (Table 2). Mean seed weight was significantly higher in the acidic herb pool (2.81 mg) as compared to the base-rich herb pool (1.21 mg), while LDW, SLA, seed number, clonality and PLH tended to be higher (although not significant) among herbs in the base-rich region. Collinearity of several traits (Spearman's rank correlation) implies restrictions for a multiple regression analysis. Seed weight was (as expected) positively correlated with plant height ($r^2 = 0.450$, $p = 0.001$) and LDW ($r^2 = 0.465$,

$p < 0.0001$), but negatively correlated with seed number ($r^2 = 0.472$, $p < 0.0001$). Plant height was also positively correlated with LDW ($r^2 = 0.680$, $p < 0.0001$).

Relationship between herb local abundance, regional distribution and traits

Although the herb sample size was small for the oceanic, acidic region (Setesdal), correlations between herb frequencies and plant traits were in general high, and some significant relationships were evident (Table 3a). The most obvious

Table 2. Differences in mean values of life history traits between regions. Bold values denote significant differences between regions (two-sample *t*-test). See text for definitions of traits * $p < 0.05$.

Sites	Parameters	Plant height	Seed number	Clonality	Seed weight	Leaf dry weight	Specific leaf area
Hol	Mean	26.4	478	1.96	1.21	56.00	28.90
	N	52	54	55	54	52	50
	SE	3.49	221.7	0.1	0.29	20.5	1.94
Setesdal	Mean	24.8	104	2.15	2.81*	39.7	26.06
	N	11	13	13	13	11	11
	SE	5.53	46.8	0.25	1.04	13.6	2.16

Table 3. Relationship between herb local abundance and regional distribution, and the plant traits of each species within (a) an acidic region (Setesdal) and (b) a base-rich region (Hol).

	Local abundance						Regional distribution					
	B	SE	<i>t</i>	r^2	df	<i>p</i>	B	SE	<i>t</i>	r^2	df	<i>p</i>
Setesdal												
Plant height	-0.052	0.054	-0.96	0.11	8	0.36	-0.173	0.091	-1.91	0.31	8	0.090
Seed number	-0.032	0.018	-1.82	0.23	11	0.09	-0.061	0.027	-2.26	0.32	11	0.045
Seed number deviation	-0.033	0.019	-1.72	0.23	10	0.12	-0.04	0.034	-1.20	0.13	10	0.26
Seed weight	0.024	0.021	1.12	0.10	11	0.29	-0.02	0.037	-0.56	0.03	11	0.58
Seed weight deviation	-0.021	0.039	-0.55	0.33	11	0.59	-0.02	0.06	-0.35	0.01	11	0.73
Leaf dry-weight	-0.023	0.041	-0.57	0.04	9	0.58	-0.06	0.071	-0.84	0.07	9	0.42
Clonality	0.092	0.032	2.92	0.46	10	0.015	0.107	0.063	1.69	0.22	10	0.12
Specific leaf-area	0.128	0.139	0.92	0.09	9	0.38	0.33	0.237	1.37	0.17	9	0.20
Hol												
Plant height	-0.019	0.028	-0.69	0.01	50	0.49	0.001	0.018	0.04	0.00	50	0.97
Seed number	-0.023	0.013	-1.76	0.06	52	0.084	-0.012	0.008	-1.49	0.04	52	0.14
Seed number deviation	-0.019	0.013	1.41	0.04	52	0.16	-0.001	0.008	-0.076	0.00	52	0.94
Seed weight	0.019	0.010	1.87	0.06	52	0.067	0.006	0.006	0.90	0.02	52	0.37
Seed weight deviation	0.014	0.03	0.47	0.00	52	0.64	0.005	0.018	0.28	0.00	52	0.77
Leaf dry-weight	0.003	0.013	0.28	0.00	50	0.78	0.008	0.009	0.97	0.02	50	0.33
Clonality	0.022	0.03	0.66	0.01	50	0.51	0.003	0.02	0.16	0.00	50	0.87
Specific leaf-area	-0.108	0.054	-1.98	0.08	48	0.053	0.012	0.037	0.33	0.00	48	0.74

Herb frequencies are arcsine transformed and traits are in-transformed prior to analyses (except clonality) The importance of each trait is analysed using linear regression.

difference as compared to the base-rich region (Ho1) was the significant positive relation between clonality and plant frequencies at the local scale (Figure 1a) and the marginally non-significant positive relation at the regional scale (Figure 1b). Seed number was negatively correlated with plant frequencies at both scales. Plant height was marginally non-significantly negatively related to regional distribution in the acidic habitat.

Seed weight and seed number were both marginally non-significantly (positively and negatively, respectively) related to local abundance

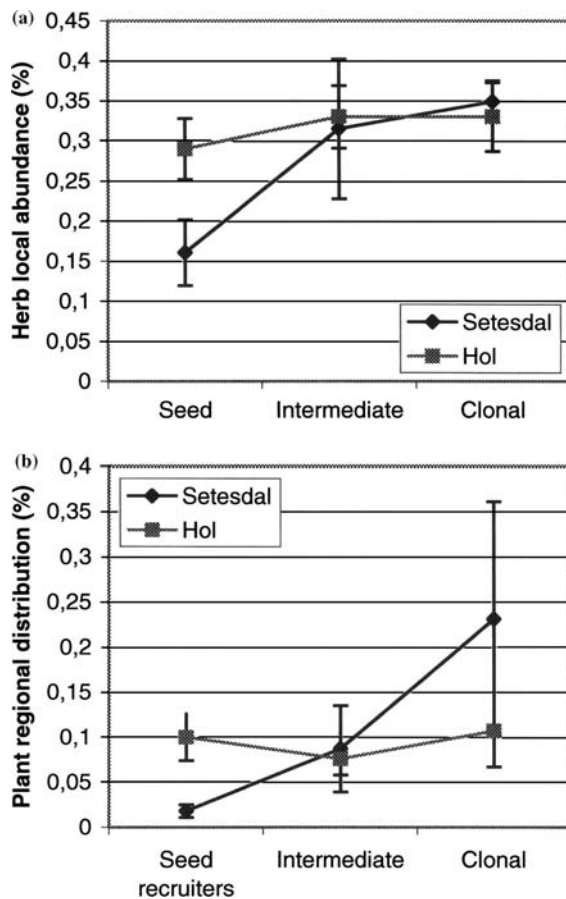


Figure 1. Herb frequencies (%) related to different recruitment strategies; (1) mainly sexual reproduction, (2) intermediate (both sexual and clonal reproduction, (3) mainly clonal reproduction. Herb frequencies are presented both at (a) local and (b) regional scales including data from both Hol and Setesdal. Error bars denote SE. See Table 3 a and b for parameter estimates.

in the base-rich region (Ho1) (Table 3b). SLA also showed a close to significant negative relationship to local abundance in the base-rich region. Seed number tended to be negatively related to regional distribution, but correlations between herb frequencies and their traits were in general weak at a regional scale in this sub-continental region. Relations between clonality and plant frequencies were weak at both scale; i.e. the frequencies of herbs mainly recruiting by seeds did not differ significantly from herbs with a vegetative reproduction (Figure 1 a; local scale and b; regional scale). Analyses of plant frequency-trait relationship using phylogenetic independent contrast showed minor differences as compared to analyses without taking phylogeny into account and are not further reported here.

Relationship between herb richness and soil variables

Soil pH was also most important environmental variable for explaining herb richness at the base-rich site ($t=22.51$, $df=179$, $p<0.0001$). Herb richness at the acidic site showed no significant correlation with any of the measured soil variables.

Relationship between herb frequencies, pH and traits

All herbs at the base-rich site with a frequency $>5\%$ (26 species) had a significant positive relationship with pH, *Hieracium alpinum* ($t=-0.533$) excepted. No herb in the acidic region with a frequency $>5\%$ (6 species) was significantly related to pH. We further examined if slope estimates (β -pH values) for each herb were correlated with their traits. Clonality was marginally non-significantly correlated with β -pH values for all species with a positive relationship to pH in the base-rich region ($t=-1.86$, $df=22$, $p=0.076$); i.e. species with clonal reproduction tended to decrease in frequency with an increase in soil pH (Figure 2). Seed weight also showed a marginally non-significant positive correlation with β -pH values ($t=1.83$, $df=21$,

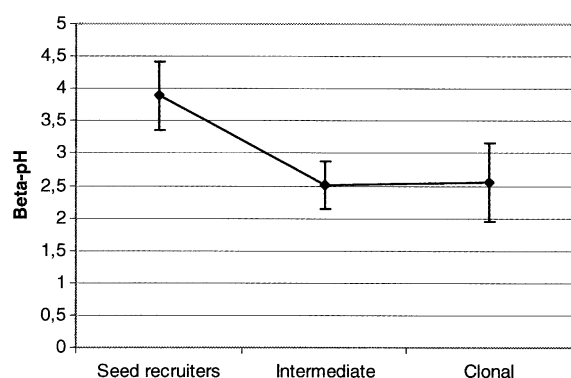


Figure 2. Relationship between β -pH values (regression coefficients for soil pH–herb local abundance relationships) and clonality. The analyses are based on the Ho1 data only. Error bars denote SE. See text for parameter estimates.

$p = 0.0818$); i.e. species with large seeds tended to have higher frequency increase with increasing pH than small-seeded species.

Discussion

Herb frequencies and plant traits

The predicted relationship between specific plant traits and frequencies examined in this study are based on the assumptions that: (1) some plant traits are correlated with plant colonisation (Weiher et al. 1999), and (2) colonisation affects herb frequencies in alpine habitats (e.g. Chambers 1993; Welling and Laine 2000; Austrheim and Eriksson 2003). We further predicted that the relative importance of recruitment traits should be higher in a low productive acidic region (Setesdal) as compared to a productive base-rich region (Ho1). The restricted herb richness at the acidic site implies a low statistical power for the plant frequency–plant trait analysis, and we only found partial evidence for such a pattern. However, herb frequency was related to reproduction strategy at both the local and the regional scale (marginally non-significant) at the acidic site; clonal species were more abundant than species recruiting through seed. Regression coefficients were also higher for every model examined in the data set from the acidic region (Setesdal) as compared to the base-rich region (Ho1).

Reproduction strategy and seed weight turned out to be the most relevant plant traits for evaluating variations in herb frequencies. Although the relative importance of different reproduction strategies is known to vary within species due to e.g. environmental harshness (Svoboda and Henry 1987), the frequencies of sexually vs. vegetatively reproducing species give a more direct measure of colonisation ability as compared to “hard” but indirect measures of SLA, LDW and plant height. The relative importance of each trait is however difficult to evaluate for the herb species pool (since few traits were significant), but several relationships were consistent between regions and scales. Seed number was negatively related (marginally non-significant) to plant frequency in both regions at a local and a regional scale. Based on the well-known trade-off between seed number and seed weight (which we also found in this study), and the key importance of seed weight (Moles and Westoby 2002), which is found to increase with habitat severity (cf. Westoby et al. 1997), the lack of significant relationships between seed weight and abundance was unexpected. However, seed weight is positively correlated with local abundance in both regions, while the decrease in importance of seed weight from the local to the regional scale was expected due to the fact that fewer seeds are available on a regional scale (Eriksson and Jakobsson 1998). Still, this study does not support the prediction that species with a low deviance from seed mass or seed number mean should have the highest abundance as suggested by Eriksson and Jakobsson (1998).

Plant height was negatively correlated with abundance in Setesdal at both scales. Westoby (1998) suggests that this trait could be useful for detecting plant adaptations to disturbance and stress. Consequently, plants should be low to be able to colonise in the low productive region of Setesdal. SLA [the equivalents of relative growth rate (RGR)] was negatively correlated with plant abundance as predicted (marginally non-significant) although this pattern was only revealed at the local scale in Ho1. This is in agreement with the results from a seed addition experiment in a subalpine habitat (Austrheim and Eriksson 2003), and plants with small but relatively thick leaves (low SLA) are generally expected to have

an advantage in stressful habitats (Reich et al. 1997; Westoby 1998). High SLA is usually correlated with favourable conditions and high competitive effort, while positive interactions could be more important in alpine environments (Callaway et al. 2002). Overall, this study shows that alpine herb communities possess large variations in several quantitative traits expected to be important for plant establishment (cf. Weiher et al. 1999), even if the number of viable life histories in tundra habitats is considered to be limited (Körner 1999).

Differences in species pool composition between regions

The most obvious difference between regions is found in herb richness. Few herb species were included in the acidic species pool ($n=13$) as compared to the non-acidic pool ($n=55$). These regional diversity patterns are affected by processes acting on both global, regional and local scales, and local plant communities are constrained by both biotic and abiotic factors that determine the species (and traits) from the available pool that can persist at a site (Austrheim and Eriksson 2001). Herbs exclusive for the Ho1 species pool have a lower seed weight, tend to be more dependent on sexual reproduction and produce more seeds as compared to the Setesdal herb pool. All, except *Gentiana pupurea* and possibly *Aconitum septentrionalis* and *Thalictrum alpinum*, also have a wide distribution within alpine habitats in Norway or wide lowland distribution with a limited altitudinal range (Lid and Lid 1994; Appendix 1). No species could be considered as rare or with a narrow geographical distribution, which is common for many alpine plants in Norway (Sætersdal and Birks 1997). Except for two oceanic species (*Narthecium ossifragum* and *Cornus suecica*), the Setesdal herb pool is a subgroup of generalists which all are present in the non-acidic region. These herbs produce larger seeds, seed production tends to be low, and strict clonal herbs tend to be more common than seed recruiting herbs. Several studies have indicated that ecological and historical processes within the latest 12–10000 years could explain the distribution of alpine plants in the Scandinavian mountains (cf.

Birks 1996; Brochmann et al. 2003). The wide distributions of the herbs exclusive for the Ho1 species pool throughout most of Norway suggest an ecological explanation to the discrepancy in species diversity between regions.

The importance of pH

Mechanistic explanations for the discrepancy in species richness between base-rich sites and acidic sites have generally been poor. However, in a recent study Pärtel (2002) found close relations between local plant richness patterns and the evolutionary history, depending on whether the species pool had its origin in a region with high or low soil pH values. Moreover, soil pH was found to be a key environmental factor at high (and low) latitudes. The species pool of Scandinavian mountain plants favoured by base-rich soils includes one third of the total alpine species pool [ca. 70 species according to Nilsson (1986) and Gjaerevoll (1990)], and 43% of the herbs exclusive for Ho1 are considered to be base-indicators (20 of 46 species with a known indicator value >5 , cf. Ellenberg 1991). Only 1 of 13 species (*Trifolium repens*) is considered to be a base-indicator in Setesdal (but this species may as well be favoured by human activities). The number of base-indicating bryophytes was also significantly higher in Ho1 as compared to Setesdal (Austrheim et al. in press). It could of course (in spite of the differences in base-indicators) be questioned if the small differences in soil pH between regions could explain the large differences in herb richness. However, Pärtel (2002) found that the positive relationship between pH and species richness is stronger at low pH levels common at high latitudes. Ca values are also significantly higher at the base-rich site than at the acidic site. High precipitation in Setesdal (and a corresponding high humidity level) might cause leaching of Ca (Kinzel 1983; Økland 1996), which could affect plant community patterns (since Ca correlates strongly with pH). Ca is considered to be a key nutrient (cf. Økland and Eilertsen 1993; Økland 1996), and higher Ca levels in Ho1 than in Setesdal indicate a higher productivity at the sub-continental, more base-rich site (Økland 1996), although other soil properties (P, K, Na, Mg) had higher

values in Setesdal (Table 1). High levels of Ca are also found to have a positive effect on species richness due to a lowered aluminium ion concentration (DeGraaf et al. 1997; Roem et al. 2002).

Alternative explanations for the discrepancy in species richness between regions should also be considered. This study showed that soil pH was a key environmental factor for herb richness only in Hol, and there was a general lack of herb richness–environment relationships in Setesdal. Correlations between environmental variables and herb plot scores along species compositional gradients obtained by Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) supported these differences in herb–environment relationships between regions (G. Austrheim unpubl). Disturbance is a possible cause for the lack of a relationship in Setesdal, and strong selection of grazing tolerant or resistant species might reduce species richness at larger scales (cf. Olff and Ritchie 1998). Average grazing pressure has been much stronger in Setesdal compared to Ho1, and low productive habitats (e.g. Setesdal) are expected to be more vulnerable to grazing as compared to a productive habitat (cf. Proulx and Mazumder 1998; Austrheim and Eriksson 2001); i.e. plant richness decreases with increasing grazing intensity when productivity is low. Soil moisture (that also differs significantly between regions) is found to be less important for plant richness patterns in alpine systems (Moe 1995; Sætersdal and Birks 1997) except for the possible indirect effects (i.e. Ca leakage, Kinzell 1983).

This study also indicates that the effect of pH on plant frequencies is related to plant life history traits as predicted. In accordance with Gough et al. (2000), we found that seed reproducing herbs tend to have higher abundances at high levels of pH as compared to clonal species. Herbs with large seeds also tend to increase their abundance with increasing pH levels, and the relative effect of these two interrelated traits is difficult to evaluate. In general, low pH is known to restrict nitrification rates, and some elements such as aluminium (Al) become toxic, which may prevent germination or plant persistence (Rorison 1960; DeGraaf et al. 1997). Roem et al. (2002) found a significant germination reduction in heathland at pH below 5. Germination was

also poor in plots where Al had been added (Roem et al. 2002).

Conclusion

Plant traits important for recruitment tend to affect local abundance and regional distribution of herbs in alpine plant communities, but the relative importance of traits is stronger at the acidic site (Setesdal) as compared to the base rich region (Ho1). Most notably, sexually regenerating species had lower frequencies as compared to clonal species in this acidic region. The prediction that herb trait–frequency relationships are sensitive to soil pH is further supported by the increase of seed recruiting species with soil pH at the base rich site. Seed weight also tended to be positively correlated with soil pH at Ho1. Studies from subalpine grasslands have shown high seed production and recruitment under favourable conditions (Chambers 1993, 1995; Welling and Laine 2000; Austrheim and Eriksson 2003), but the relative importance of sexual reproduction for plant richness in alpine habitats is unclear. This study suggests that recruitment is critical for the species pool composition (herb local abundances and regional distribution) in a harsh alpine region, while species recruit more independently of traits in the productive region. Possible ecological explanations for recruitment constraints include both soil acidity (low pH and Ca levels in addition to possible aluminium toxicity) and disturbance through grazing. Seed addition experiments with measures of plant recruitment and with grazing and soil pH as factors are needed to test the relative importance of these alternative predictions.

Acknowledgements

We wish to thank Inger E. Måren and Janne Wilhelmsen for help with collecting field data in Setesdal, and Erika Leslie for analysing soil samples. Rune H. Økland, Kristian Hassel and an anonymous referee gave valuable comments on the manuscript. The study received financial support from the Research Council of Norway, project no. 134361/720.

Appendix 1. Total herb species pool in Hol and Setesdal. Information on plant systematics, traits and β -pH values are given for each species.

Nr	Species	Family	Life-form	Distribution	pH-ind	Dist set	Abu Set	Dist Hol	Abu Hol	Plant height (cm)	No. of seeds	Seed weight (mg)	LDW (mg)	SLA (mm ² /mg)	RS	Ref. On clo.
1	<i>Aconitum septentrionale</i>	Ranunculaceae	Perennial	AlpLowR			1.7	0.2	1.7	131.7	95.9	1.811	452.7	85.6	1	5
2	<i>Alchemilla alpina</i>	Rosaceae	Perennial	AlpC	2		16.0	9.5	16.0	8.2	25.0	0.362	4.6	11.3	2	1
3	<i>Antennaria alpina</i>	Asteraceae	Perennial	AlpC			1.1	0.2	1.1	13.8	151.2	0.105	2.1	29.0	3	1
4	<i>Antennaria dioica</i>	Asteraceae	Perennial	AlpLowC	3		2.2	0.1	2.2	15.7	373.5	0.123	4.2	17.1	3	1,2
5	<i>Astragalus alpinus</i>	Fabaceae	Perennial	AlpC	6		0.6	0.4	0.6	11.8	58.0	1.614	1.8	15.9	2	1
6	<i>Bartsia alpina</i>	Scrophulariaceae	Perennial	AlpC	7		4.4	1.5	4.4	20.3	333.0	0.177	10.4	18.9	3	1
7	<i>Bistorta vivipara</i>	Polygonaceae	Perennial	AlpLowC	4		30.9	13.2	30.9	19.0	23.8	1.685	7.1	21.1	3	1
8	<i>Campanula rotundifolia</i>	Campanulaceae	Perennial	AlpLowC	0		7.2	1.6	7.2	21.3	6.5	0.042	3.1	28.6	3	1
9	<i>Cerastium alpinum</i>	Caryophyllaceae	Perennial	AlpC	6		0.6	0.1	0.6	8.7	9.9	0.052	1.7	19.7	2	1
10	<i>Cerastium cerastoides</i>	Caryophyllaceae	Perennial	AlpC	4		5.0	1.5	5.0	7.8	26.2	0.204	0.3	52.2	2	1
11	<i>Cerastium fontanum</i>	Caryophyllaceae	Perennial	AlpLowC	5		0.6	0.1	0.6	21.0	24.3	0.194	3.0	24.9	2	1
12	<i>Cirsium helenioides</i>	Asteraceae	Perennial	AlpLowC			0.6	0.2	0.6	100.3	127.5	3.562	855.4	15.0	2	6
13	<i>Coeloglossum viride</i>	Orchidaceae	Perennial	AlpLowC	4		1.7	0.2	1.7	17.2	10000	0.000	13.4	32.4	1	5
14	<i>Cornus suecica</i>	Cornaceae	Perennial	AlpLowR	2	11.0	3.9			14.9	2.5	8.407	11.8	23.4	3	5
15	<i>Crepis paludosa</i>	Asteraceae	Perennial	AlpLowC	8		1.7	0.8	1.7	60.4	85.9	0.362	75.0	40.9	2	6
16	<i>Epilobium angaldifolium</i>	Onagraceae	Perennial	AlpC	5		3.3	1.3	3.3	10.6	59.5	0.059	1.1	34.6	2	6
17	<i>Euphrasia frigida</i>	Scrophulariaceae	Annual	AlpC	3		12.2	3.7	12.2	10.0	44.0	0.183	1.2	20.5	1	
18	<i>Fragaria vesca</i>	Rosaceae	Perennial	LowC	0		0.6	0.0	0.6	37.3	341.00	0.346	150.5	22.2	3	2,3
19	<i>Gentiana purpurea</i>	Gentianaceae	Perennial	AlpR	3	1.5	0.2			54.7	432.1	0.069	209.1	19.2	1	5
20	<i>Geranium sylvaticum</i>	Geraniaceae	Perennial	AlpLowC	6		26.5	12.2	26.5	69.5	24.8	4.537	492.5	28.0	1	1
21	<i>Geum rivale</i>	Rosaceae	Perennial	LowC	2		0.6	0.1	0.6	22.5	298.3	0.811	24.7	25.2	1	3
22	<i>Hieracium alpinum</i>	Asteraceae	Perennial	AlpC	1	0.5	0.0	24.9	4.6	13.4	94.3	0.582	6.1	25.4	3	4
23	<i>Hieracium</i> sp.	Asteraceae	Perennial	AlpLowC			0.6	0.1	0.6	22.4	13.0	0.104	12.6	31.0	1	4
24	<i>Leontodon autumnalis</i>	Asteraceae	Perennial	AlpLowC	5		7.2	2.5	7.2	16.7	40.2	0.756	3.0	18.6	1	4
25	<i>Lotus corniculatus</i>	Fabaceae	Perennial	LowC	7		3.9	0.7	3.9	5.0	30.2	0.435	9.1		3	3
26	<i>Matianthemum bifolium</i>	Convallariaceae	Perennial	LowC	3	8.0	3.2	2.2	1.4	22.5	7.1	6.006	14.2	19.5	1	
27	<i>Melampyrum pratense</i>	Scrophulariaceae	Annual	LowC	3	1.5	0.3	0.6	0.1	19.1	11.0	5.886	5.9	24.9	1	
28	<i>Melampyrum sylvaticum</i>	Scrophulariaceae	Annual	LowC	2		12.7	2.9	12.7	44.6	38.8	0.285	9.9	47.1	2	1
29	<i>Myosotis decumbens</i>	Boraginaceae	Perennial	AlpC	5		1.1	0.1	1.1	20.0	500.0	0.1	18.8	19.9	3	5
30	<i>Narthecium ossifragum</i>	Melanthiaceae	Perennial	LowR	2	1.0	0.3			27.3	1423.0	0.078	19.6	28.9	2	6
31	<i>Omalotheca norvegica</i>	Asteraceae	Perennial	AlpC	4		18.8	4.1	18.8	7.5	117.9	0.090	2.0	39.7	2	1
32	<i>Omalotheca sapina</i>	Asteraceae	Perennial	AlpC	3		11.0	4.4	11.0	18.9	393.0	0.014	11.6	26.8	2	6
33	<i>Parnassia palustris</i>	Saxifragaceae	Perennial	AlpLowC	7		2.2	0.4	2.2	13.5	36.7	0.192	6.0	21.2	3	1
34	<i>Pedicularis lapponica</i>	Scrophulariaceae	Perennial	AlpC			8.8	3.3	8.8	10.7	226.9	0.019	5.6	52.9	1	5
35	<i>Pinguicula vulgaris</i>	Lentibulariaceae	Perennial	AlpLowC	7		1.1	0.1	1.1	23.8	52.1	0.631	5.4	23.6	2	1
36	<i>Potentilla erecta</i>	Rosaceae	Perennial	AlpLowC	8		1.7	0.2	1.7	24.8	26.6	0.459	7.5	22.1	1	2,4
37	<i>Potentilla minor</i>	Rosaceae	Perennial	LowC	0	4.0	1.0	8.8	3.7	17.3	5000.0	0.0007	28.5	19.0	3	1
38	<i>Pyrola minor</i>	Pyrolaceae	Perennial	AlpLowC	3		13.8	4.9	13.8	22.3	5000.0	0.001	84.4	12.4	2	1
39	<i>Pyrola rotundifolia</i>	Pyrolaceae	Perennial	AlpLowC	5		5.0	1.7	5.0	47.4	66.1	1.566	39.2	26.9	2	1,4
40	<i>Ranunculus acris</i>	Ranunculaceae	Perennial	AlpLowC	0		18.2	6.6	18.2							

Appendix 1. Continued.

Nr	Species	Family	Life-form	Distribution	pH-ind	Dist set	Abu Set	Dist Hol	Abu Hol	Plant height (cm)	No. of seeds	Seed weight (mg)	LDW (mg)	SLA (mm ² /mg)	RS	Ref. On clo.
41	<i>Ranunculus platamifolius</i>	Ranunculaceae	Perennial	AlpC	0		0.6	0.1	44.5	27.4	5.108	135.6	28.4	1	5	
42	<i>Rhinanthus minor</i>	Scrophulariaceae	Annual	AlpLowC	0		2.2	0.4	22.9	45.2	1.927	5.6		1		
43	<i>Rubus chamaemorus</i>	Rosaceae	Perennial	LowC	2	22.0	7.3	1.7	0.6	11.5	10.6	43.538	90.8	16.4	3	5
44	<i>Rumex acetosa</i>	Polygonaceae	Perennial	LowC	0	2.0	0.8	35.4	12.4	72.0	176.5	1.016	65.7	32.8	2	4
45	<i>Sagina procumbens</i>	Caryophyllaceae	Perennial	AlpLowC	7		3.3	0.5	2.1	51.0	0.012	0.2		2	6	
46	<i>Sagina saginoides</i>	Caryophyllaceae	Perennial	AlpC	5		1.7	0.1	4.7	105.0	0.022	0.3	41.0	2	6	
47	<i>Saussurea alpina</i>	Asteraceae	Perennial	AlpC	5		13.3	3.4	53.3	5.5	2.057	64.3	32.8	3	1	
48	<i>Sibbaldia procumbens</i>	Rosaceae	Perennial	AlpC	2		13.8	5.3	4.3	32.0	0.502	10.3	15.5	2	1	
49	<i>Silene dioica</i>	Caryophyllaceae	Perennial	LowC	7		2.2	0.4	59.1	220.0	0.931	34.8	33.9	2	5	
50	<i>Solidago virgaurea</i>	Asteraceae	Perennial	AlpLowC	0	6.0	0.8	23.2	3.9	32.1	17.3	0.460	27.2	31.9	2	1
51	<i>Stellaria borealis</i>	Caryophyllaceae	Perennial	AlpR			0.6	0.2	29.9	98.9	0.150	2.5	51.3	2	6	
52	<i>Taraxacum</i> sp.	Asteraceae	Perennial				12.2	4.3		9.2	0.537			1	1	
53	<i>Thalictrum alpinum</i>	Ranunculaceae	Perennial	AlpR			3.3	0.9	16.7	9.2	0.537	11.7	17.6	3	1	
54	<i>Trifolium europaea</i>	Primulaceae	Perennial	LowC	3	67.0	24.3	48.1	21.8	9.1	2.2	0.165	10.0	36.5	3	1
55	<i>Trifolium repens</i>	Fabaceae	Perennial	LowC	6	1.5	0.2			64.0	0.228			3	2	
56	<i>Veronica alpina</i>	Scrophulariaceae	Perennial	AlpC	0		10.5	1.6	12.6	282.0	0.054	2.9	20.3	2	1	
57	<i>Veronica fruticans</i>	Scrophulariaceae	Perennial	AlpC	0		1.1	0.6	8.0	39.4	0.099	3.3	14.9	2	1	
58	<i>Viola biflora</i>	Violaceae	Perennial	AlpC	7		27.1	15.4	9.3	9.0	0.0698	6.9	54.8	1	1	
59	<i>Viola palustris</i>	Violaceae	Perennial	AlpLowC	2	18.0	7.1	11.0	3.5	5.4	15.7	0.352	15.0	36.7	2	6

Distribution: AlpC = alpine common. AlpR = alpine restricted. LowC = lowland common. LowR = lowland restricted. AlpLowC = both alpine and lowland distribution and common. AlpLowR = both an alpine and lowland distribution but restricted. pH-ind. = Indicator values of base-richness in the soil are given by Ellenberg et al. (1991). Local abundance: AbuSet = local abundance Setesdal. AbuHol = local abundance Hol. DistSet = regional distribution Setesdal. DistHol = regional distribution Hol. Plant traits: SLA = specific leaf area. LDW = leaf dry weight. RS = reproduction strategy: 1 = mainly sexual reproduction. 2 = both sexual and clonal reproduction. 3 = mainly clonal reproduction. References on reproduction strategy: (1) Söyinki 1938, (2) Eriksson and Jakobsson 1998, (3) Dupre and Ehrlén 2002, (4) Grime et al. 1988, (5) Austrheim unpubl., (6) no specific reproduction strategy are registered for these species and all are thus considered to have a limited clonal reproduction.

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