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The Impact of Disturbance and Seed Availability on Germination of Alpine Vegetation in the Scandinavian Mountains

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Abstract

The availability of seeds and microsites are limiting factors for many plant species of different vegetation types. We have investigated the existence of such limitations in two habitats, an alpine heath and a subalpine birch forest, where abiotic factors are hypothesized to be the main determining factor of plant species distributions. Both habitats are characterized by a short growing season and cold temperatures, and the alpine heath is also constrained by low productivity. A seed addition experiment including six vascular plants, selected by different functional traits and occurrence, showed that seed limitation was an important factor in these habitats. Removal of the aboveground biomass (controlled disturbance) increased germination only for some species. The effect of reindeer presence was found to be of less importance, probably due to low and varying densities of reindeer. To conclude, we found that seed limitation was the most important factor limiting the distribution of our studied species in the two alpine environments.

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Introduction

Germination, and thereby population dynamics, for many species of different types of vegetation is limited by the availability of seeds (Turnbull et al., 2000) and by suitable microsites for seeds to germinate in. Seed limitation and microsite limitation may act in combination if germination is favored not only by seed addition but also by small-scale disturbances (e.g. Eriksson and Ehrlén, 1992; Jakobsson and Eriksson, 2000; Eskelinen and Virtanen, 2005). We found it especially important to study limitations for germination in plant species in alpine and subalpine environments where plant distributions often are assumed to be structured by abiotic factors (Körner, 2003). Sexual reproduction is stochastic, and alpine plants experience large variation among years in both seed production and seedling establishment (Chambers, 1995; Larsson and Molau, 2001). Even though sexual reproduction is rare and many plants rely on vegetative propagation and have a capacity for being long-lived (Jonsdottir et al., 2000), occasional seedling recruitment is important for maintaining genetic diversity of populations and for colonization of previously unoccupied sites (Eriksson, 1993). In closed vegetation microsite availability might be enhanced by mammals, e.g. trampling by reindeer (*Rangifer tarandus*) and digging by rodents (Moen et al., 1993). Such disturbances may have positive effects on some plant species, by creating gaps for recruitment in a dense vegetation cover, or have negative effects when the disturbance is extensive, resulting in bare soil patches (Austrheim and Eriksson, 2001; Klug et al., 2002; Cairns and Moen, 2004; Olofsson et al., 2004, 2005). Biotic interactions among plants might influence seedling germination both positively by facilitation and negatively by competition (Dormann and Brooker, 2002; Olofsson, 2004). Facilitation among species exists if the establishment and growth of a species is enhanced by the presence of other species, and some studies indicate that the importance of facilitation increases in harsh environments (Wipf et al., 2006). However, other studies have shown that competition could be an important factor limiting the establishment of plant species in alpine environments, and the relative importance of facilitation and competition will vary across gradients of abiotic stress (Maestre et al., 2005).

The alpine heath is dominated by a vegetation cover consisting of a dense layer of ericaceous shrubs with low productivity, while the vegetation cover in the subalpine birch forest is dominated by birch, herbs, grasses, mosses, and liverworts, with relatively high nutrient availability. We studied the importance of seed availability and microsite availability for the germination of six selected vascular plant species in these two habitats. Although the presence and density of reindeer is variable between years and grazing and trampling effects are extensive in the study area, we expect reindeer presence to enhance germination by the creation of small gaps and by reducing the accumulation of litter (Virtanen, 2000). In addition, we recorded seedlings of other species, present in the vicinity of the study area but not included in the seed addition experiment, in order to assess the importance of reindeer presence and disturbance for natural seedling recruitment.

Methods

STUDY SPECIES AND SITES

Six species were used in the sowing experiment (Table 1). Henceforth they are referred to by their generic names. The species were selected based on their functional traits such as life span, seed size, dispersal mode, and occurrence in order to get a subset of species with a wide spectrum of different traits. None of the species is known to have an extensive persistent seed bank.

The study sites were situated in the vicinity of Ammarnäs, southern Lapland, Sweden (66°N, 16°E). Two sites were located above the tree line on the alpine heath, at an altitude of 800–1100 m a.s.l., and two sites were located in the subalpine birch forest, at an altitude of 500–650 m a.s.l. The heath sites were dominated by mosses, lichens, dwarf shrubs, grasses, and sedges. The birch forest sites were situated in humid slopes where tall

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TABLE 1

The species used in the sowing experiments, their life forms, seed weights, dispersal attributes, and the most characteristic habitat. Data collected from field sampling or literature (Grime et al., 1988; Peat and Fitter, 2005).

Species	Life form	Seed weight (mg)	Dispersal unit (vector)	Habitat
Vaccinium myrtillus	dwarf shrub	0.26	fleshy fruit (animals)	alpine heaths
Empetrum hermaphroditum	dwarf shrub	0.75	fleshy fruit (animals)	alpine heaths
Rhinanthus minor	annual herb	2.84	winged seed (wind)	grasslands
Rumex acetosa	perennial herb	0.74	winged seed (wind)	grasslands
Cicerbita alpina	perennial herb	0.09	achene with pappus (wind)	birch forests
Trollius europeus	perennial herb	1.12	achene (unspecialized)	birch forests

herbs dominated the shrub layer. Mosses, liverworts, *Vaccinum myrtillus*, graminoids, and small herbs were significant constituents of the herb layer. All four sites were inhabited by free ranging reindeer (*Rangifer tarandus*) during the summer season, with densities varying between years.

Forage selection by reindeer at landscape level is mainly determined by forage biomass, predation, and insect harassment (Rettie and Messier, 2000; Mårell et al., 2002; Skarin et al., 2004). Once in the vicinity of the experimental plots, reindeer could be attracted to the plots by curiosity or avoid the plots because of a lack of biomass, but forage patch selection is mainly shown to be structured by forage quality, and the experimental plots are too small to alter the food quality of the sites.

EXPERIMENTAL DESIGN

At each site, a large reindeer exclosure (100 m × 100 m) was built in 1996. Close to each exclosure, an equivalent control area where reindeer had access was chosen. In each of the exclosures and in the control areas, 40 plots of the size of 20 cm × 20 cm were placed (10 per treatment). The experiment with artificial disturbance and seed addition consisted of four different treatments: seeds added/not added combined with plots disturbed/not disturbed. In total, about 32,000 seeds from each of the experimental species were collected in the study area (seeds of *Rhinanthus* were collected in the vicinity of the village of Ammarnäs). The seed addition treatment consisted of sowing a seed mix in 1999 of 200 seeds of each of the six investigated species per 4 dm^2 plot, based on the findings of Lindborg (2006), where it was shown that 50 seeds dm^{-2} per species was an optimal seed density. Since the germination rate was relatively low and since the germination of naturally occurring seeds was independent of the seed addition experiment (see Results), direct interactions between seeds and/or seedlings can be regarded as negligible. Seeds from fleshy fruits were extracted before sown. All seeds were distributed immediately after collection. The disturbance treatment consisted of the removal of all aboveground vegetation before seed addition in 1999 and was not repeated the following years since it risked removing seeds/seedlings and since there were not much inward growth from the perimeters.

The experiment was initiated in August 1999 and the seedlings emerging in the plots were recorded at the end of July for three years (2000–2002). Since it was not possible to follow seedlings individually, the response variable analyzed, "germination," was the total number of emerging seedlings within the three years. Double counting could be avoided because aged seedlings can be distinguished from recent ones. In addition to the experimental species, seedling emergence of other species was also recorded in order to assess the importance of grazing and disturbance for natural seedling recruitment. It should be noted that we have no information on the seed availability of the species recruiting naturally in the plots.

Due to low recruitment, and thus many zeros in the database for plots without seed addition, the intended use of a split-plot ANOVA was not feasible. Therefore, we divided the analyses into two steps, where we first tested if the presence of reindeer affected seed germination with a Mann-Whitney U-test. In this test, we used the pooled data from both habitats, both sites in each habitat, and for both seed addition and disturbance treatments. In the cases where reindeer presence had no effect, we analyzed the effect of the treatments on the pooled data from both the control (reindeer present) and the exclosures (reindeer absent) with a Generalized Linear Model with a Poisson distribution. In the cases where reindeer presence had a significant effect (*Trollius*), we analyzed the effect of the treatments separately with data from the exclosures and outside the exclosures, respectively (see Table 2). The number of seedlings was square-root-transformed before analysis, but the figures are based on back-transformed data. Data on seedlings of other species were analyzed in the same way as *Trollius*, since reindeer presence had an effect on the germination of other species. Data on seedlings of other species is collected only from the birch forest since there were very few seedlings of other species germinating in the alpine heath.

Results

Our results indicate that the presence of reindeer do not have a strong effect on the germination of seedlings of the experimental species, except for *Trollius europeus*, where germination was more successful inside the reindeer exclosures (Table 2 and Fig. 1) Five species (all except *Empetrum*) germinated in the birch forest and all of those were favored by seed addition (Table 3). Only three species germinated in the alpine heath, two of which, *Rumex* and *Vaccinium*, were favored by seed addition (Table 3). Removal of aboveground biomass increased germination for *Rumex* and *Vaccinium* (Table 3, Figs. 1 and 2). There were differences in germination between the two habitat types, since *Trollius*,

TABLE 2

The effects of reindeer presence on the germination of the six species included in a seed addition experiment (N = 160) and other seedlings, and *Ranunculus acris* (N = 80), tested with Mann-Whitney U-tests. Significant results are in bold.

	Z	P
Vaccinium	0.753	0.451
Empetrum	0.967	0.334
Rhinanthus	0.462	0.644
Rumex	0.347	0.729
Cicerbita	−0.685	0.493
Trollius	−2.113	**0.035**
Other species	−2.273	**0.023**
Ranunculus acris	−3.744	**<0.001**

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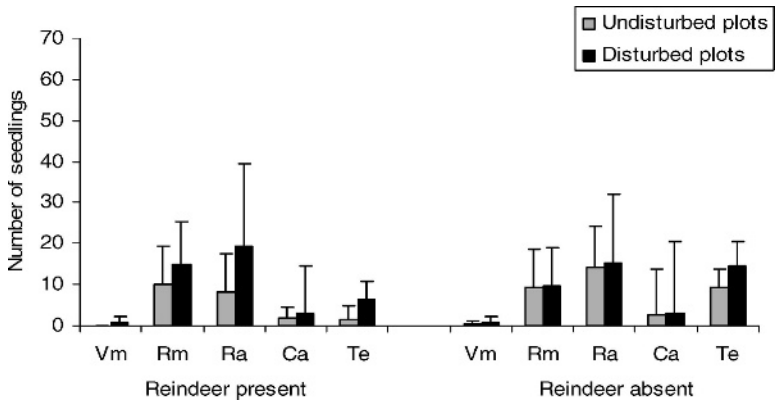


FIGURE 1. The germination of *Vaccinium myrtillus* (Vm), *Rhinanthus minor* (Rm), *Rumex acetosa* (Ra), *Cicerbita alpina* (Ca), and *Trollius europeus* (Te) in the subalpine birch forest, with and without reindeer in plots where seeds were added. Error bars are denoted by 1 sd.

TABLE 3

The effects of habitat, seed addition, and disturbance on the study species where reindeer presence was not of significant importance for germination, analyzed with a Generalized Linear Model (GLZ) with Poisson distribution. Significant results are in bold.

	DF	Log-Likelihood	Chi-Square	*p*
Vaccinium				
habitat	1	−349.7	1.335	0.248
seed	1	−344.8	9.715	**0.002**
disturbance	1	−342.6	4.434	**0.035**
habitat × seed	1	−341.7	1.700	0.192
habitat × disturbance	1	−341.6	0.352	0.553
seed × disturbance	1	−340.4	2.343	0.126
habitat × seed × disturbance	1	−340.3	0.215	0.643
Rhinanthus				
habitat	1	−396.0	88.762	**<0.001**
seed	1	−351.6	88.762	**<0.001**
disturbance	1	−351.3	0.595	0.441
habitat × seed	1	−332.3	38.069	**<0.001**
habitat × disturbance	1	−332.2	0.223	0.637
seed × disturbance	1	−332.1	0.117	0.732
habitat × seed × disturbance	1	−332.1	0.072	0.788
Rumex				
habitat	1	−497.3	11.026	**0.001**
seed	1	−393.3	208.092	**<0.001**
disturbance	1	−387.7	11.216	**0.001**
habitat × seed	1	−387.5	0.428	0.513
habitat × disturbance	1	−387.0	0.824	0.364
seed × disturbance	1	−386.4	1.343	0.247
habitat × seed × disturbance	1	−386.0	0.782	0.376
Cicerbita				
habitat	1	−340.0	20.290	**<0.001**
seed	1	−336.7	6.628	**0.010**
disturbance	1	−336.6	0.111	0.739
habitat × seed	1	−334.6	3.980	**0.046**
habitat × disturbance	1	−334.6	0.066	0.798
seed × disturbance	1	−334.5	0.081	0.776
habitat × seed × disturbance	1	−334.5	0.051	0.822
Empetrum				
habitat	1	−308.5	0.248	0.618
seed	1	−308.3	0.248	0.618
disturbance	1	−308.3	0.185	0.667
habitat × seed	1	−308.1	0.233	0.630
habitat × disturbance	1	−308.1	0.174	0.677
seed × disturbance	1	−308.0	0.163	0.686
habitat × seed × disturbance	1	−307.9	0.154	0.695

Rhinanthus, and *Cicerbita* seedlings only emerged in the birch forest. *Empetrum* germinated only in the alpine heath, but in very low numbers. *Rumex* and *Vaccinium* germinated in both habitats, with *Rumex* more strongly in the alpine heath than in the birch forest.

Germination of other species in the birch forest was negatively influenced by reindeer presence (Table 2 and Fig. 1). One of the most common species among those other species, *Ranunculus acris*, was also negatively influenced by reindeer presence. The seed addition experiment did not affect germination of these naturally occurring seedlings, but the removal of biomass increased the germination of other species both inside and outside the reindeer exclosure. *Ranunculus acris* benefited from disturbance inside the exclosure, but was unaffected outside the exclosure, where reindeer had access.

Discussion

Reindeer presence did not have any significant positive effects on seedling emergence, as has been shown in other studies (Fig. 3) (i.e. Eskelinen and Virtanen, 2005). The densities of reindeer in the study area are highly variable and we could not observe any obvious trampling effects in the immediate vicinity of the experimental plots during the study period, but we could observe selective grazing on large herbs in the birch forest. Compared to the artificial disturbance, the disturbance effects by reindeer (trampling) were probably much smaller. The grazing effects by reindeer could be severe for the preferred species, but the density of reindeer was probably too low to generate effects such as a decrease of litter and aboveground biomass. The number of seedlings of other species and *Trollius* were negatively influenced by reindeer presence (Table 4), which could be due to selective grazing, as we did see that reindeer often preferred reproductive parts of the plants (Mårell et al., 2002), and thus could decrease the amount of seeds locally (Cooper and Wookey, 2003).

In contrast to disturbances by reindeer, the controlled disturbance, where the aboveground biomass was removed, had significant positive effects on some species, indicating that competition from other plant species limit the availability of suitable microsites for those species. Gough (2006) also found that seed germination rates were significantly higher in an arctic plant community where mosses and vascular plants were removed compared to plots with intact vegetation. Three of the species only occurring in the birch forest, *Rhinanthus*, *Trollius*, and *Cicerbita*, were not affected by disturbance, and similar results were found for *Rhinanthus* also in a study by Austrheim and Eriksson (2003). Seed weight and recruitment have been found to be positively correlated (Westoby et al., 1997; Turnbull et al., 1999) and large-

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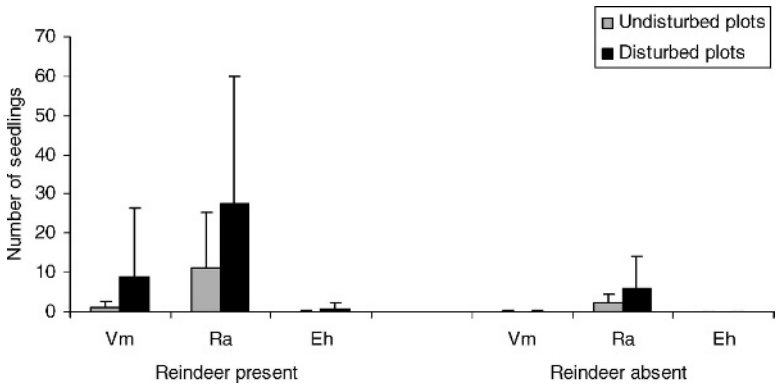


FIGURE 2. The germination of *Vaccinium myrtillus* (Vm), *Empetrum hermaphroditum* (Eh), and *Rumex acetosa* (Ra) in the alpine heath, with and without reindeer in plots where seeds were added. Error bars are denoted by 1 sd.

seeded, non-clonal species are successful in the phase of seedling emergence even in closed vegetation, as large seeds allow them to emerge, effectively disregarding competition from other species (Welling and Laine, 2002). However, the light seeds from *Cicerbita* and the intermediate-sized seeds from *Trollius* (see Table 1) also showed the same pattern, which is harder to explain by the seed weight. *Rhinanthus* is hemiparasitic, and the availability of suitable host plants could affect the survival, but probably not the germination, of *Rhinanthus* seedlings. The low importance of small-scale disturbance could be due to the structure of the vegetation in the birch forest. The vegetation cover is very dense in the shrub layer, while the ground is only patchily covered by small herbs, grasses, and mosses, which may make the small-scale disturbance of the ground layer in this study of less importance in the birch forest.

Another structuring force in plant communities might be seed limitation (Tilman, 1997), and one definition of seed limitation is an increase in population size following seed addition (Turnbull et al., 2000). However in this study, we did not follow the demography of the species, so our definition of seed limitation is an increase in seedling density after seed addition (see also Austrheim and Eriksson, 2003). With this definition in mind, all species were seed limited to some extent except for *Empetrum*, were no seeds germinated in the birch forest and very few on the alpine heath. A close relative to *Empetrum hermaphroditum*, *E. nigrum*, has been shown to be a bad colonizer by Olofsson et al. (2005). In their study, *E nigrum* failed to colonize gaps even though it dominated the undisturbed vegetation. Another study of the genetics of different clones indicates that *E. hermaphroditum* establishes by seeds to a relatively large extent over a long time span (Szmidt et al., 2002). *Empetrum* has also been shown to produce biologically active phenolic compounds that can limit the establishment of other species (Shevtsova et al., 2005). *Trollius*, *Cicerbita*, and *Rhinanthus* were seed limited in the birch forest, and *Vaccinium* and *Rumex* were seed limited in both habitats. Seed limitation is also confirmed among alpine and arctic plants by recent studies of snow bed communities (Eskelinen and Virtanen, 2005) and arctic tundra plant communities (Gough, 2006). None of the species included in this study has any verified extensive seed bank longevity. Some studies of other species indicate that extensive seed banks may exist in alpine environments (e.g. Ingersoll and Wilson, 1993; Diemer and Prock, 1993; Cavieres, 1999; Welling and Laine, 2002), but there are few studies on seed bank longevity from the Scandes. There were almost no seedlings emerging from the experimental species in the plots without seeds added, indicating a seed limitation of those species. However, there were a relatively high number of seedlings of other species in the birch forest, which indicates a high occurrence of other seeds in the soil in the birch forest, especially from *Ranunculus acris*. The species not recruiting in the alpine heath are probably constrained by other factors than seed limitation and microsite availability, i.e. abiotic factors.

In conclusion, the subalpine birch forest and the alpine heath are differing in the germination rate of most species. Seed limitation is by far the most important factor in both habitats, while disturbance plays a more crucial role in the alpine heath. Reindeer presence does not significantly influence five of the six study species, but for *Trollius* and naturally germinating species in the plots, reindeer presence was negative for seed germination, probably due to selective feeding on reproductive parts of the plants.

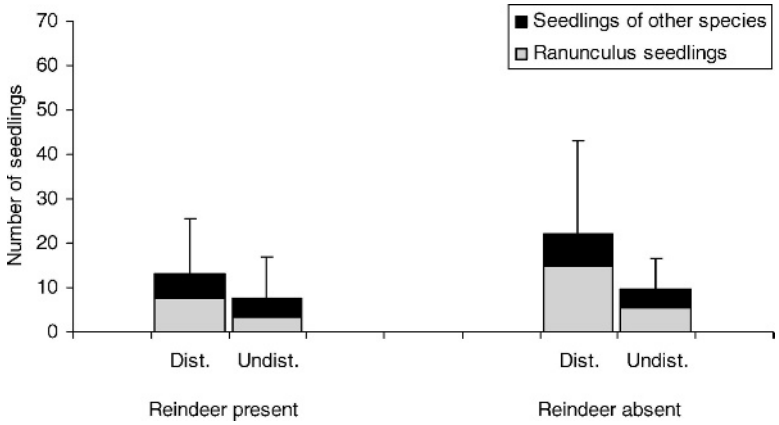


FIGURE 3. The effect of disturbance in the plots on the total number of seedlings from species not included in the seed addition experiment in the subalpine birch forest, with and without reindeer. "Dist." means disturbed plots and "Undist." means undisturbed plots. The proportion of *Ranunculus* seedlings are marked in the bars. Error bars are denoted by 1 sd for all seedlings.

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TABLE 4

The effects of habitat, seed addition, and disturbance on germination of *Trollius* and the effects of seed addition and disturbance on germination of other species, and *Ranunculus acris*, with and without reindeer presence, analyzed with a Generalized Linear Model (GLZ) with a Poisson distribution. Significant results are in bold.

	DF	Log-Likelihood	Chi-Square	*p*	DF	Log-Likelihood	Chi-Square	*p*
Trollius	Reindeer present				Reindeer absent			
habitat	1	−176.7	10.944	**0.001**	1	−201.4	50.807	**<0.001**
seed	1	−173.0	7.343	**0.007**	1	−185.5	31.936	**<0.001**
disturbance	1	−171.8	2.387	0.122	1	−184.7	1.488	0.223
habitat × seed	1	−169.6	4.412	**0.036**	1	−178.5	12.370	**<0.001**
habitat × disturbance	1	−168.9	1.401	0.236	1	−178.3	0.531	0.466
seed × disturbance	1	−168.8	0.197	0.657	1	−178.3	0.016	0.900
habitat × seed × disturbance	1	−168.8	0.134	0.714	1	−178.3	0.008	0.930
Other seedlings								
seed	1	−106.997	1.298	0.255	1	−108.325	2.205	0.138
disturbance	1	−104.860	4.274	**0.039**	1	−102.796	11.058	**0.001**
seed × disturbance	1	−104.289	1.141	0.285	1	−102.345	0.901	0.343
***Ranunculus* acris: reindeer present**								
seed	1	−117.457	2.047	0.153	1	−112.815	2.446	0.118
disturbance	1	−115.753	3.410	0.065	1	−107.119	11.393	**0.001**
seed × disturbance	1	−115.683	0.140	0.708	1	−107.030	0.177	0.674

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