MASTER THESIS IN ECOLOGY

REINDEER GRAZING HISTORY EFFECTS ON

PLANT RECRUITMENT AND LIFE HISTORY TRAITS FROM

THE GERMINABLE SEED BANK.

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I have called this principle,
by which each slight variation,
if useful, is preserved, by the
term Natural Selection.

-Charles Darwin-

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ABSTRACT

Seed banks represent a source from which new vegetation may quickly arise if the existing stand is disturbed. It is increasingly discussed that reindeer grazing modifies the seed banks in northern ecosystems. However no large-scale studies have been carried out to support this hypothesis. Because reindeer could constitute a selective pressure on vegetation recruitment, the present study investigated seed banks in terms of plant life history traits (i.e. life form, growth form, diaspore morphology, and seed weight) in paired areas with a similar long term history of grazing but contrasting reindeer densities during the last 20 years in Finnmark (Norway).

In this study, 63 species geminated from the seed banks, while seed bank densities varied from 575 to 3 506 seeds m^2 per area independent of reindeer density. Reindeer density did not affect the presence of any plant life history trait in the seed banks, with graminoids, hemicryptophytes, and small (0-0.5 mg) and unappendaged seeds being the most abundant traits under both density regimes. Moss layer thickness was negatively correlated with the seed bank density, indicating it could constitute a mechanical barrier for the input of seeds to the seed bank. The results from this study do not show an effect of a short term increase in reindeer densities, whereas they are consistent with a seed bank trait composition expected from vegetation with a long term grazing history.

INTRODUCTION

Natural selection imposes a reproductive strategy on each species by favouring those life-history traits that enable an organism to survive and transmit its genes to the next generation (Stearns 1995). In plants, seed production is one of the most important strategies for survival and propagation (Fenner and Thompson 2005). Within a landscape, the success of a seed depends on both the seed's traits, e.g. seed size or diaspore morphology, and environmental factors, e.g. moss layer thickness, seed predators, and litter cover.

Seeds disperse as seed rain on to top vegetation and litter cover (Chambers and MacHahon 1994, Jutila 1998, Márquez et al. 2002) and accumulate in the soil forming a seed bank (Chippindale and Milton 1934, Thompson 1987, Fenner and Thompson 2005). Seed banks constitute a large genetic pool where different genotypes are expected to do well in different years, with different environmental patterns (Fenner and Thompson 2005). Therefore, seed banks become an important adaptable and regenerative factor for the vegetation in a disturbed and variable environment such as a grazed ecosystem (Chippindale and Milton 1934, Chambers and MacHahon 1994, Welling et al. 2005). Nevertheless, studies connecting seed banks to vertebrate grazing, agree that grazing changes the composition of the seed bank (Chippindale and Milton 1934, O´Connor and Pickett 1992, Jutila 1998, Mayor et al. 2003, Sternberg et al. 2003, Eskelinen and Virtanen 2005). In Scandinavia, few grazing studies have taken seed banks into account, even though Scandinavia has a long tradition of livestock grazing, which is defining for plant diversity patterns (Austrheim and Eriksson 2003).

Reindeer husbandry in Norway is managed within units called districts, which support different reindeer densities. The semi-domestic reindeer (*Rangifer tarandus tarandus*) survive on the nutrient poor common grounds on the continental plain during winter, while their growth and reproduction depends on nutrient rich vascular plants that dominate summer grounds along the coast (Skjenneberg and Slagsvold 1968). The number of reindeer has increased in northernmost

Norway from 53 180 in 1950 to nearly 200 000 in 1990 (Danell et al. 1999). Furthermore, it has been claimed that the actual reindeer densities in Finnmark are not sustainable for the ecosystem (Moen and Danell 2003).

Classification of plants according to life history traits has a long tradition in plant ecology. Ecologists are becoming increasingly aware of the need to find common spatio-temporal patterns displayed by plants in response to specific disturbance regimes (McIntyre et al. 1999, Rusch et al. 2003). Individual traits are changed on an ecological time scale by external factors such as grazing or mowing (Zobel 1992). Milchunas et al. (1988) argued that the response of vegetation to grazing depends on the evolutionary history of grazing in the given community. Consequently, grazing could be considered a disturbance if it deviates from the conditions under which the community has developed (Hobbs 1996). However, grazing selects for entirely different traits than abiotic disturbances, like landslides or floods, where frequently all individuals are eliminated (Oksanen and Virtanen 1997). Grazers such as reindeer, are known to pick their food non-randomly (White and Trudell 1980, Warenberg 1982). It has been documented that reindeer actually choose flower-dense patches and select if available fruits and flowers because of their higher nutritional quality (Wada 1999, Cooper and Wookey 2003). Furthermore, several studies show that reindeer grazing reduces both the abundance of preferred forage plants and the presence of inflorescences (Klein 1990, Wada 1999, Bråthen and Oksanen 2001, Cooper and Wookey 2003). If selection of flowers and fruits by reindeer is too high, the production of seeds could be reduced, which ultimately can be expected to modify the composition and number of successful plant traits in the seed banks.

In addition to reindeer grazing, the surrounding physical environment of the seed bank also influences its composition. Moss layer thickness has been found an important barrier for seed input to the soil seed bank and an inhibitor of seed germination (reviewed by During & van Tooren 1990). Litter has been found a good seed accumulator (Jutila 1998, Márquez et al. 2002). However, it also has negative effects both by being a mechanical barrier for seed input and by decreasing the amount of light for germination (Facelli and Pickett 1991, Foster and Gross 1998).

The present study considers in addition to moss layer thickness and litter cover, two plant traits and two seed traits that could be important for seed banks in relation to vertebrate grazing.

Growth forms have been considered a good indicator of grazing intensity. Graminoid growth forms are the most adapted to moderate ungulate grazing conditions (Post and Klein 1996). Graminoids seem to respond positively to ungulate grazing in a wide range of environments, from Arctic areas (Wegener and Odasz-Albrigtsen 1998) to African savannas (McNaughton 1984). Shrubs are less able to respond positively to grazing and have been found to die back in favor of graminoids in heavily reindeer visited areas due to trampling (Olofsson 2006). Dicotyledons generally suffer from a higher degree of herbivory; thus, their seed output can be reduced (see for example Ehrlén 1997).

Life forms sensu Raunkiaer (1934) are influenced by grazing pressure. Phanerophytes and chamephytes have their growing buds above ground level, while hemicryptophyte plants have them at soil level. This difference in meristem location can favor hemicryptophytes, because they have their growing buds less exposed to grazers. Grazing also reduces competition from taller species allowing hemicryptophytes to take advantage of open space (McIntyre et al. 1995).

Different *diaspore morphologies* allow for a variety of mechanisms of seed dispersal. Some seeds simply drop to the ground, others blow through the air on tiny "wings", others are moved through water, and still others are encased in fruits and have to survive a trip through the animal's digestive system before they germinate. Diaspores provided with hooks or awns will disperse attached to animal fur. When a diaspore has appendages, its probability of entering the soil seed bank decreases (Rabinowitz 1981) but, simultaneously, its chances of landing in the correct standing orientation for germination increase (Peart 1981, 1984, Welling et al. 2004).

Finally, s*eed mass* is associated with the successful establishment of the seedling. Large seeds have more stored nutrients and better competitive ability in closed vegetation, or in a seedling crowded environment (Westoby et al. 1992). On the other hand, small seeds are more easily dispersed, better colonizers of bare soil, less detected by predators, and more able to enter and accumulate in the soil seed bank (Thompson 1987).

It is hypothesized in this study that reindeer density could constitute a selective pressure on plant regenerative traits. To test this, reindeer herding districts were paired according to their history of reindeer density, with each pair containing both a low density district and a high density district. The opportunity to develop a study with both a temporal (i.e. a system with contrasting history of grazing intensities) and spatial (i.e. large-scale design) dimension in a non-experimental way is not common. As such, this seed study represents a pioneering approach. Moss layer thickness and litter cover measurements were included because of their likely importance in reducing seed recruitment. This study hypothesizes that 1) seed bank densities and species richness are reduced in high reindeer density areas; 2) reindeer density shapes the presence of the different traits in the seed bank; and 3) seed density is reduced as moss layer thickness and litter cover cover increases.

MATERIAL AND METHODS

1. Study design

This study was carried out in the reindeer summer districts of Finnmark, Northern Norway, between the latitude, 77°91'N-30°90'E and 78°54'N-64°28' (Figure 1). The study sites were located in the low alpine zone, where snow cover remains til late June and the main vegetation types are grass meadows and *Empetrum* and *Vaccinium* dominated heaths and marsh (Moen 1998). The main herbivores are large grazers as reindeer (*Rangifer tarandus tarandus* L.), moose (*Alces alces*), and locally domestic sheep (*Ovis canadensis)*. Also widespread are Norwegian lemmings (*Lemmus lemmus* L.), ptarmigan (*Lagopus lagopus*), and grey sided voles (*Clethionomys rufocanus)*.

Finnmark is divided in 40 reindeer herding districts and has been naturally grazed by reindeer for centuries (Danell et al. 1999). For this study, districts were paired according to their history of reindeer density. The two districts forming a pair had maintained constant their reindeer numbers from the 1950's until the 1980's, after which, one of the districts in the pair increased its density 100 to 200% (i.e. high reindeer density district), while the other district maintained its density constant (i.e. low reindeer density district) (Anonymous 2004) (Table 1). Faeces counts from the different studied districts confirmed that high reindeer density districts had a higher animal density (Iversen et al. unpublished). Furthermore, both districts forming a pair had to be neighbouring districts in order to eliminate climatic and geoedaphic differences (*sensu* Kruckeberg 2002). Under these criteria, only three pairs of districts were identified. The three pairs were by chance located in three different Finnmark regions (Figure 1). Therefore, environmental regional differences were expected between the pairs (e.g. altitude, climate, slope, and bedrock).

Table 1. District identification number (ID) and mean reindeer density (reindeer km^2) in each district and days available in the summer grazing grounds

REGION	District ID Reindeer density	Mean Reindeer Density 1943-1980	Mean Reindeer Density 1980-2003
West Loppa Kommune	27 High density	3.2	12.1
	28 Low density	3.2	3.2
Middle Hammerferst Kommune & Kvalsund Kommune	20 High density	4.5	7.1
	21 Low density	4.7	4.7
East Varanger-halvøya	6 High density	1.1	2.5
	7 Low density	1.4	1.7

Table 2. Nested study design, including the number of visited blocks, study areas, transects and plots per district. Number of gathered samples per district is also included.

LEVELS		*Level 1*	*Level 2*	*Level 3*	*Level 4*	*Level 5*		
	Region	Reindeer density	Blocks	Study Areas	Transects	Plots	Soil cores Collected	Top layer samples Collected
	West	High	6	9	23	50	46	50
		Low	6	9	21	54	53	54
	Middle	High	6	13	29	66	66	66
		Low	6	13	31	68	68	67
	East	High	8	16	41	93	93	93
		Low	5	10	27	54	54	54
TOTAL	3	6	37	70	172	385	380	384

Table 3. Precipitation and temperature mean for June, July and August 2004 and the normal for the last 30 years (Meteorologisk.Institut 2006)

| REGION	2003		2004		Normal (1961-1990)	
	Precipitation (mm)	Temperature (ºC)	Precipitation (mm)	Temperature (ºC)	Precipitation (mm)	Temperature (ºC)
WEST	52.4	10	45.8	11.1	61.4	10.6
MIDDLE	55.2	12.1	56.3	14.3	54.4	10
EAST	47.3	9.2	45.9	10.8	49.4	8.9
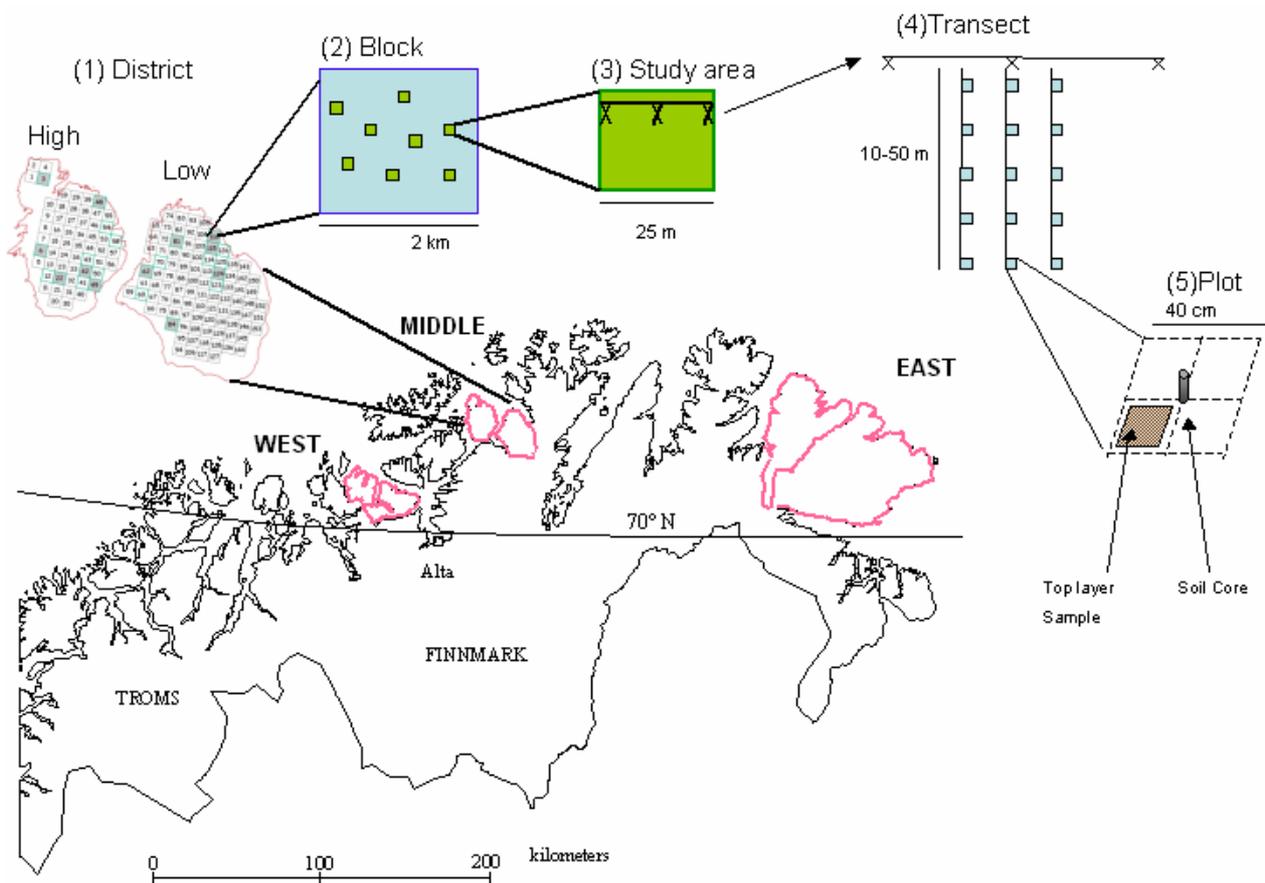
Figure 1. Location of the studied pairs of districts located in three regions, i.e. west, middle, and east Finnmark, and division of the each district in hierarchical levels. First in blocks (blue blocks were those visited during this study), then study areas with the three GPS coordinates showing the orientation of the study area. Each study area was divided into transects and finally in plots where a soil core and a top layer sample were collected. See study area and design chapter for details.

Each district was further divided into nested levels (Table 2). The first division was in blocks of 2 x 2 km^2. Blocks containing major roads, sea, lakes, glaciers, or more than 50 % forests were discarded due to their low probability of reindeer visitation.

Each block was divided in study areas. The further selection of study areas was based on topographic curvature, slope, and altitude above sea level (asl). Areas with concave curvature accumulate moisture and nutrients, hence they were assumed to have a larger productivity and therefore, to attract reindeer. Only study areas with a mean slope between 7.5° and 30° (between 5° and 30° in the eastern region which is less steep) were chosen. Terrain above 600 m asl in west Finnmark, above 500 m asl in mid Finnmark, and above 300-350 m asl in eastern Finnmark, was not included. Altitudinal belts above these heights generally represent the middle to high alpine zone, which contains sparse vegetation. Potential study areas were located

selecting pixels with the specified concave curvature, slope and altitude from a terrain model using GIS software (ArcGIS 2004). Each study area was located in the field with geographical coordinates (longitude and latitude) provided by the GIS programme.

Those blocks that contained the largest number of potential study areas were visited. Once located in the field, the study area had to meet certain conditions. First, the vegetation cover had to be higher than 75%. Second, the study area had to include a shift between at least two of the three following types of vegetation: ridge vegetation (dry, low vegetation), leeside vegetation (mesic, herbs, graminoids, ericoids and shrubs), and snowbed vegetation (mesic to wet vegetation, no major presence of ericoids). And third, the study site had to be large enough to include at least two transects (each no less than 10 meters long) and should not contain paths, electric posts, marsh, or bog.

If a study area failed to meet any of these conditions, it was discarded and the one closest to it was visited and inspected for possible analysis. If none of the potential study areas suggested by the terrain model satisfied the conditions, a new subjective study area was chosen taking into account the above selection criteria. Once the study area was selected, between two and five transects were laid out down slope with a 5 meter separation between them (Figure 1), starting in the ridge/heath area. Soil cores and top layer samples were gathered every tenth meter of each transect in order for data to be representative of the area. If the plot had more than 50% stones, it was discarded and the plot in the next two meters was taken instead. If that plot also failed to meet the conditions, the plot two meters before the original plot was taken. If none of those options was successful, the sample was not colleted. The amount of gathered samples per study area varied between 2 and 14.

Districts in the same pair were sampled simultaneously in order to avoid differences in plant phenology. Data was assembled over four weeks, starting on week 30 in the Western part of Finnmark, during July and August 2004. At that time, some current year seeds had maybe already dispersed. It is therefore possible the samples contained both transient seeds, i.e. with a life span of less than a year, and persistent seeds, i.e. at least 1 year old (Thompson et al., 1997). The

summer temperatures and precipitation from the 2004 and 2003 summer months are given as the average of June, July, and August (Table 3). Plant nomenclature follows Lid & Lid 1994.

2. Data collection

Litter cover measurements were taken every tenth meter of the transect following the Point Intercept Method (PIM) (Levy and Madden 1933), modified according to Bråthen and Hagberg (2004). Moss layer thickness was measured with a ruler in the highest and lowest corners of the plots at every tenth meter (Figure 2).
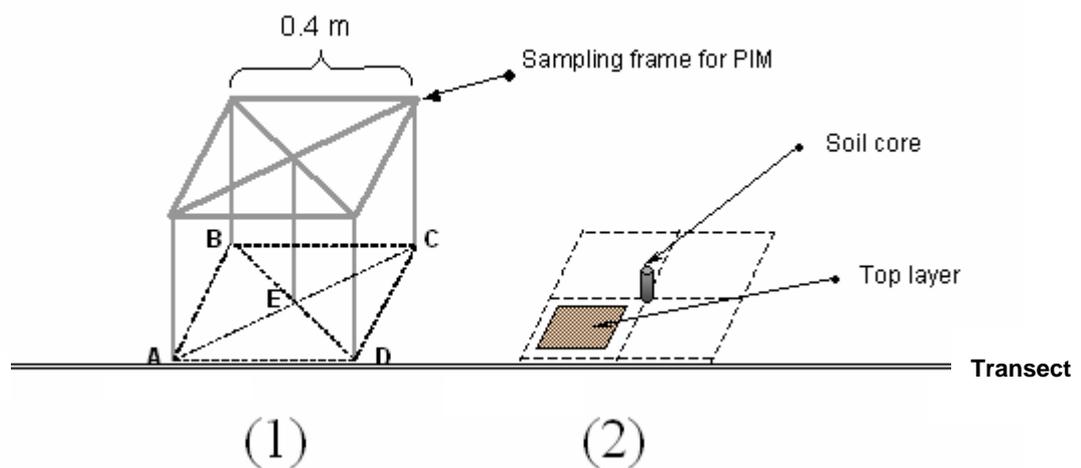
Figure 2. Plot analysis and sample collection was done every tenth meter. First step (1): Measurements of moss thickness taken at the corners **B** and **C** of the plot, while litter cover was measured as hits with the pins of the sampling frame (points **A** to **E**). Second (2), soil core and top layer samples were taken. See data collection section for details.

A 2.5 cm diameter soil core was collected with a 10 cm long metal cylinder placed down at soil level, below the humus layer, in the centre of the studied plot. The core depth varied in accordance with the thickness of the organic soil layer of the plot. Top layer samples, i.e. vegetation cover down to the humus layer, including moss layer and litter cover, were taken by collecting a 15 x 15 cm sample from one of the corners of each studied plot (Figure 2). The soil core represents the soil seed bank while the top layer sample represents the seed rain of the

present year and of a few previous years. Soil cores and top layer samples were stored in paper bags until they were frozen no later than 8 hours after collection. Samples were frozen at −18°C in order to simulate a stratification period. After 2 months, they were taken out to thaw in dark chambers at 2°C before the experiment started. A total of 380 soil core samples and 384 top layer samples were collected from the 70 visited study areas.

Soil cores were crumbled onto petri dishes (diameter 8.7 cm, depth 1.4 cm) provided with a filter paper to keep the moisture. A third part of every top layer sample was put in a transparent box (20x15 cm), also with filter paper. All samples were randomly placed in two phytotron chambers which simulated optimal germination conditions of most northern alpine plants: 24 hours of daylight split into 12 hours at 20°C and 12 hours at 15°C (Granström 1988, Myers et al. 2004). All samples were kept moist by water spraying every third day. Emerged seedlings were transplanted to seedling boxes and kept until identification was possible. After four months, all samples were set in refrigerated dark chambers at 2 °C in order to simulate a winter period. Soil cores were crumbled again and returned together with the top layer samples to the growth chambers for the germination to continue after three weeks of chilling. Nitrate is the major naturally occurring inorganic soil component that stimulates seed germination (Bewley 1997, Alboresi et al. 2005). Therefore, samples were sprayed after the second chilling period once a week, during two weeks, with KNO_3 (10mM) (Karssen and Hilhorst 1992, Batak et al. 2002, Giba et al. 2003). Seedling emergence was monitored during a total of seven months, until no more seedlings emerged from the samples. Seedlings dying before identification were classified in general groups: dicotyledon, graminoid, or ericoid shrub. When not even that was possible, they were recorded as "plant". Some graminoids were cold treated (0.5 °C) to initiate flowering, in order to identify them. Measurements of soil pH were taken from every petri dish, with the help of pH papers. The range in pH was between 3 and 5 in all the regions. All samples were set up at the same time and received the same conditions and treatment during the germination period.

Slope and altitude information were taken from the terrain model. Data on the major categories of bedrock types and sediment deposits (Geological.Survey.of.Norway 2004) were

collected per study area. Bedrock nutrient content was classified into three categories: poor, moderate, and rich based on Tarbuck and Lutgens (1992).

The seed and plant traits in this study were chosen for their potential variable response to grazing (Table 4). Information on the seed traits (i.e. seed weight and diaspore morphology), and the plant traits (i.e. life form and growth form) was gathered from several sources, including online databases (Fitter and Peat 1994, Klotz et al. 2002), books (Grime et al. 1988, Lid and Lid 1994, Thompson et al. 1997), articles (Welling and Laine 2002, Welling et al. 2004), and my personal measurement and observation at the seed archive at Tromsø University Museum. For species classification after traits see Appendix 1.

Table 4. List of traits encountered in the seed bank

LIFE HISTORY TRAITS			
GROWTH FORM	LIFE FORM	DIASPORE MORPHOLOGY	SEED WEIGHT
Graminoid	Phanerophyte	No appendages	0-0.1 mg
Dicotyledon	Chamaephyte	Pappus	>0.1-0.5mg
Shrub/ericoid	Hemicryptophyte	Hooks	>0.5-1 mg
	Geophyte	Fruits	>1-5 mg
		Wings	
		Elaisome	

3. Statistical analysis

The effect of reindeer density and region (the design variables) and of moss layer thickness and litter cover amount (the covariates) were tested against a) seed bank densities, b) seed bank species richness and c) abundance of seed bank species' life history traits. Reindeer density was a categorical variable with two levels: high or low. Region had three categories, west, middle, and east. Altitude, slope, and bedrock, which were potential covariates, were confounded with the design variable region, having a strong regional gradient from east to west (Figure 3). Therefore, only the variable region was included.
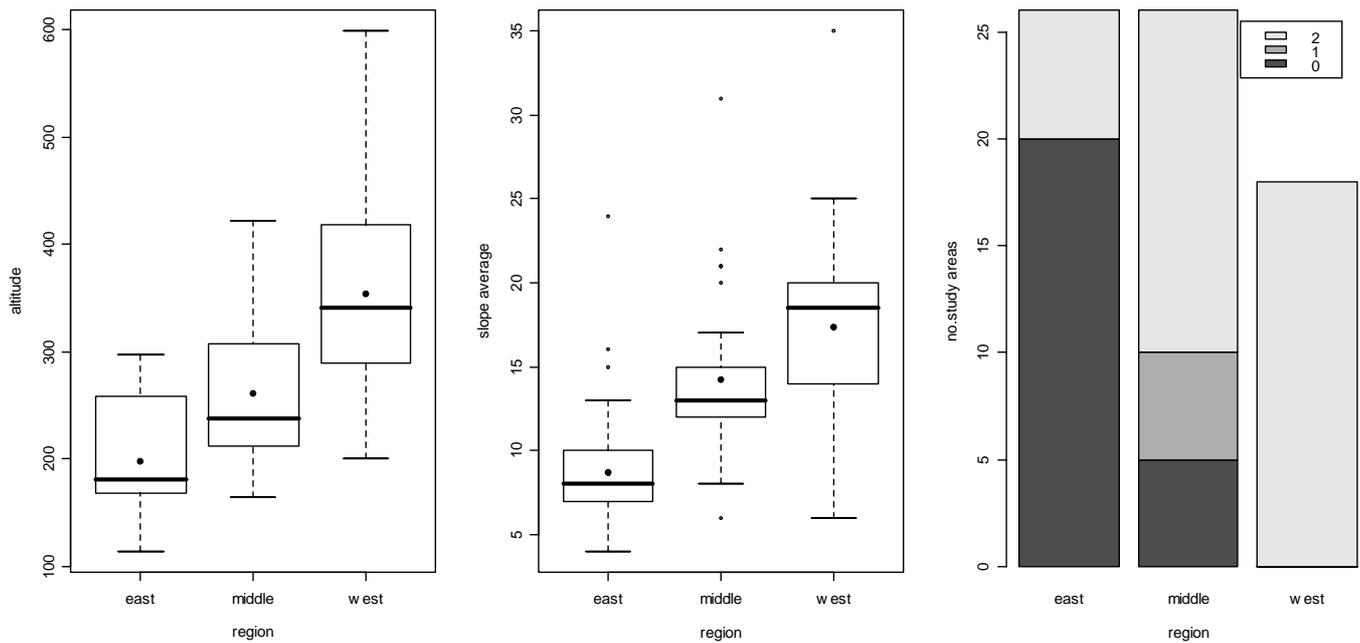
Figure 3. Environmental explanatory covariates confounded with region. A) Altitude as mean meters per study area above sea level, B) Mean slope per study area in inclination degrees, and C) Bedrock, 0= poor; 1= moderate; 2= rich. Box plots are provided with 95 % CI, the mean (dot) and the median (line).

Moss layer is presented as the mean thickness (in centimetres) of the two measurements taken at the plot level. The litter variable is presented as cover, using the mean number of frame pins that hit the litter cover (minimum 1 [20% cover], maximum 5 [100% cover]).

For the analysis, the original seedling germination results were multiplied with a conversion factor to express results as seeds per square meter; in our study, the conversion factors were 2040 and 133, for soil cores and top layer samples, respectively. For the statistical analysis, soil seed bank and top layer samples were summed together because of the large amount of zeros present in the soil seed bank data. Diaspore morphologies were grouped for the analysis in four groups: unappendaged diaspores, appendaged diaspores (hooks, fruits, elaisome, wings and pappus), animal dispersed diaspores (hooks, fruits and elaisome), and wind dispersed diaspores (wings and pappus).

All data were sampled at the plot level and were then averaged to the study area level because of the high variation in number of plots per study area. The basic study unit is thus, the study area. Data were log-transformed because they contained large number of zeros. and analysed using linear mixed effects models (lme) (Pinheiro et al. 2005) with the statistical package R (R.Development.Core.Team 2005). Lme models allow the usage in nested designs of explanatory variables that are a mixture of fixed effects and random effects (Crawley 2003). District and block were considered random effects in the model, while everything else, i.e. reindeer density, region, moss layer thickness and litter cover were taken as fixed variables. Statistical output from the lme model is presented on the logarithmic scale.

RESULTS

1. Total seed bank density and species richness

Altogether 2056 individuals germinated at the phytotron from the seed bank samples, 259 belonging to the soil seed bank and 1797 to the top layer sample. When averaged up to seeds per m^2, the top layer contained 32% of the total amount of germinated individuals, while the soil contained 67%. Seed densities did not differ between reindeer densities (Table 5). The most abundant seed bank density was found in the middle region, which had 3 times more seeds than the other regions (Table 5, Appendix 2).

A total of 63 species germinated from the total seed bank, which constituted only 28 % of the 187 species found aboveground (Ravolainen et al. unpublished).

Twenty-two species were identified from the soil seed bank, while 62 were found in the top layer sample. *Juncus filiformis* was the only species absent from the top layer but present in the soil. Most species absent from the soil seed bank but present in the top layer had appendaged diaspores (24 out of 37 species).

Total seed bank species richness did not differ between reindeer densities (Table 5). Fifty-two species were identified in high animal density areas, while there was 56 germinating from low reindeer density areas. There was a significant difference in seed bank species richness between regions. The seed banks from the middle region were the most rich, followed by the west region, and finally the eastern region (Table 5).

When looking at the seed bank species richness, *Carex brunnescens* was the most abundant in both high and low reindeer density areas (Appendix 3). Next in high reindeer areas was*, Carex lachenalii*, *Vaccinium myrtillus* and *Empetrum nigrum spp. hermafroditum* while it was *Cerastium cerastoides*, *Carex lachenalii* and *Sagina saginoides* in low reindeer density areas (Appendix 3).

All species encountered were polycarpic and with the exception of *Betula pendula* all had both clonal and sexual reproduction at some point in their life cycle (Klimeš et al. 1997).

The most important covariate was moss layer thickness for both species richness and seed density (Table 5). The thicker the moss layer the less species and seeds in the seed bank.

All statistical analyses were also performed with species counts instead of seed densities in order to check that the results were not an artifact of *Carex* individuals being so abundant (Appendix 1). The species lme model results were very similar to those with seed densities, presenting the same significant variables. Therefore only results from seed density analyses were presented.

Table 5. Results from a linear mixed effects model for (1) seed bank species richness, and (2) seed bank density.

Parameters	(1) Species richness				(2) Seed density			
a) Fixed effects	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|
Intercept	0.51	0.20,0.81	31	<0.01	5.38	3.49,7.27	31	0
Region middle vs. east	0.62	0.19,1.06	2	0.02	2.77	0.14,5.41	2	0.04
Region west vs. east	0.32	-0.15,0.80	2	0.09	1.77	-1.10,4.65	2	0.11
Reindeer density low vs. high	0.13	-0.23,0.51	2	0.24	0.38	-1.83,2.61	2	0.52
Moss layer	-0.20	-0.35, -0.06	31	<0.01	-1.08	-1.97, -0.21	31	0.01
Litter cover	-0.003	-0.09,0.08	31	0.92	0.08	-0.42,0.60	31	0.73
b) Random effects								
				No. Obs.=70				No. Obs.=70
~1|district				No. Gr.=6				No. Gr.=6
St. Deviation (Intercept)	0.02				0.01			
~1|block				No. Gr.=37				No. Gr.=37
St. Deviation (Intercept)	1.39				0.01			
Residuals	2.17	1.72,2.73			2.13	1.79,2.53		

2. Traits in the seed bank

Reindeer density had no effect on the seed density of any plant trait. Moss layer thickness was negatively correlated with the seed density of most traits. The model also showed very little variation explained at the district and block level of the study design, i.e. the study area level explained most variation.

2.1 Growth form

No significant effect of reindeer density was found on growth form (Table 6). The highest seed density corresponded to graminoids, then shrubs/ericoids and finally dicotyledons. Graminoids showed the highest seed bank species richness, followed by dicotyledons and shrubs/ericoids (Appendix 4). Dicotyledons had a low seed presence in the seed bank of all regions although their richness was similar to that found in graminoids (Appendix 4).

The middle region contained a larger amount of graminoids than the other two regions (Table 6). Moss layer thickness was found to have a negative effect only on graminoid seed densities (Table 6).

Table 6. Result from a linear mixed effects model for growth form (1) Graminoids, (2) Dicotyledons, and (3) Shrubs/ericoids

Parameters	GROWTH FORM											
	(1) Graminoid				(2) Dicotyledon				(3) Shrub/ericoids			
a) Fixed effects	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|
Intercept	3,62	1.33,5.93	31	<0.01	2,03	-0.2,4.24	31	0.07	3,98	1.59,6.37	31	<0.01
Region middle vs. east	3,38	-0.25,7.02	2	0.05	2,12	-1.80,6.04	2	0.14	0,62	-3.20,4.45	2	0.55
Region west vs. east	2,15	-1.68,5.99	2	0.13	1,98	-2.08,6.05	2	0.17	0,72	-3.32,4.77	2	0.52
Reindeer density low vs. high	0,78	-2.26,3.83	2	0.38	0,97	-2.28,4.23	2	0.32	0,90	-2.29,4.09	2	0.34
Moss layer	-1,16	-2.20, -0.12	31	0.02	-0,03	-0.98,0.92	31	0.94	-0,62	-1.65,0.41	31	0.22
Litter cover	-0,10	-0.68,0.48	31	0.72	-0,31	-0.84,0.23	31	0.25	-0,34	-0.94,0.27	31	0.26
b) Random effects												
			No. Obs.=70				No. Obs.=70				No. Obs.=70	
~1|district			No. Gr.=6				No. Gr.=6				No. Gr=6	
St. Deviation (Intercept)	0.02				0.42				0.51			
~1|block			No. Gr.=37				No. Gr.=37				No. Gr.=37	
St. Deviation (Intercept)	1.39				1.43				0.37			
Residuals	2.18	1.72,2.73			1.93	1.48,2.52			2.46	1.95,3.09		

2.2 Life form

Hemicryptophyte and geophyte seeds were summed because of the few germinated geophyte seeds. In combination, they were the most abundant in the seed bank, with their seed densities being negatively influenced by moss thickness (Table 7). Hemicryptophyte and geophyte seeds were significantly more abundant in the middle pair (Table 7).

Chamaephytes were the next most common growth form (Table 7). Moss layer thickness and litter cover influenced neither phanerophytes nor chamaephytes.

Table 7. Result from a linear mixed effects model for life form (1) Chamæphyte, (2) Phanerophyte, and (3) Hemicryptophyte+ geophyte.

	LIFE FORM										
Parameters	(1) Chamæphyte				(2) Phanerophyte				(3) Hemicryptophyte + geophyte		
a) Fixed effects	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|
Intercept	2.86	0.73,4.97	31	0.01	2.45	0.75,4.13	31	<0.01	4.12	1.86,6.35	31	<0.001
Region middle vs. east	1.70	-1.54,4.93	2	0.15	-0.32	-2.69,2.04	2	0.61	3.20	-0.18,6.58	2	0.05
Region west vs. east	2.26	-1.19,5.70	2	0.10	-0.35	-2.93,2.24	2	0.61	1.90	-1.70,5.51	2	0.15
Reindeer density low vs. high	1.04	-1.67,3.76	2	0.24	0.21	-1.78,2.21	2	0.69	0.85	-1.98,3.69	2	0.32
Moss layer	-0.58	-1.55,0.40	31	0.23	-0.36	-1.15,0.44	31	0.36	-1.14	-2.17, -0.10	31	0.03
Litter cover	-0.08	-0.63,0.47	31	0.77	-0.42	-0.88,0.04	31	0.07	-0.15	-0.73,0.43	31	0.60
b) Random effects											
			No. Obs.=70				No. Obs.=70				No. Obs.=70
~1|district			No. Gr.=6				No. Gr.=6				No. Gr.=6
St. Deviation (Intercept)	0.02				0.02				0.04		
~1|block			No. Gr.=37				No. Gr.=37				No. Gr.=37
St. Deviation (Intercept)	1.07				0.01				1.06		
Residuals	2.13	1.66,2.71			1.92	1.61,2.27			2.27	1.8,2.85	

2.3 Diaspore morphology

Seeds with no appendages were the most widespread in all regions and in both high and low reindeer densities (Appendix 4). Next in abundance were diaspores with pappus, followed by seeds with hooks, and then fruits. The appendaged diaspores grouped together and the unappendaged diaspores were significantly affected by moss layer thickness in the same negative direction (Table 8). Seeds provided with pappus and wings were grouped as wind dispersed diaspores, but no significant effect was found for any of the variables (Table 8). *Betula nana* seeds formed 90% of the wind dispersed diaspores.

Fruits, seeds with hooks, and elaisomes were grouped together as animal dispersed diaspores. High animal density areas did not hold a higher amount of animal dispersed diaspores, but there was a difference between regions (Table 8). Moss layer thickness had a strong negative effect on the seed density of these diaspores.

2.4 Seed mass

Seeds with a weight between 0.1 and 0.5 mg showed higher seed bank densities and species richness than lighter and heavier seeds both in the high and the low reindeer density areas (Table 9, Appendix 4). Moss layer thickness strongly influenced the abundance of intermediate size seeds (0.1-1 mg) in the seed bank (Table 9). Small seeds (0-0.1 mg) had a negative correlation with the litter cover (Table 9). This was the only trait influenced by the litter cover. The more litter cover, the less small seeds. Big seeds (0.5-1 mg) had low species richness (Appendix 4). Seeds weighting over 1mg were poorly represented in the seed bank.

Table 8. Result from a linear mixed effects model for diaspore morphology (1) seeds with no appendages (2) all seeds with appendages, (3) wind dispersed seeds (wings+pappus), and (4) animal dispersed seeds (hooks+ fruits+ elaisome).

	DIASPORE MORPHOLOGY															
Parameters	(1) Seeds with no appendages				(2) Seed with appendages				(3) Seeds wind appendages				(4) Seeds animal appendages			
a) Fixed effects	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|
Intercept	3.09	0.59,5.60	31	0.01	4.73	2.76,6.70	31	0	4.11	1.78,6.44	31	<0.01	1.52	-0.47,3.51	31	0.13
Region middle vs. east	3.26	-0.59,7.10	2	0.06	2.22	-0.50,4.94	2	0.07	0.70	-2.52,3.92	2	0.44	2.79	0.03,5.55	2	0.04
Region west vs. east	2.37	-1.71,6.45	2	0.12	1.38	-1.60,4.35	2	0.18	-0.12	-3.63,3.40	2	0.89	2.40	-0.61,5.41	2	0.07
Reindeer density low vs. high	0.84	-2.39,4.06	2	0.38	0.29	-2.00,2.59	2	0.63	0.39	-2.32,3.10	2	0.60	0.65	-1.67,2.98	2	0.35
Moss layer	-0.97	-2.12,0.17	31	0.09	-1.08	-1.99, -0.16	31	0.02	-0.51	-1.58,0.57	31	0.34	-0.99	-1.91, -0.07	31	0.03
Litter cover	-0.07	-0.71,0.57	31	0.82	-0.11	-0.64,0.42	31	0.67	-0.42	-1.05,0.20	31	0.17	0.42	-0.12,0.95	31	0.12
b) Random effects																
~1|district			No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6	
St. Deviation (Intercept)	0.02				0.01				0.02				0.01			
~1|block			No. Gr.=37				No. Gr.=37				No. Gr.=37				No. Gr.=37	
St. Deviation (Intercept)	1.34				0.06				0.03				0.16			
Residuals	2.45	1.94,3.11			2.21	1.84,2.63			2.6	2.19,3.09			2.22	1.74,2.83		

Table 9. Result from a linear mixed effects model for seed weight (1) seed weight 1 (0-0.1mg) (2) seed weight 2 (0.1-0.5mg) (3) seed weight 3 (0.5-1mg) and (4) seed weight 4 (1-5mg)

	SEED WEIGHT															
Parameters	(1) Seed weight 1				(2) Seed weight 2				(3) Seed weight 3				(4) Seed weight 4			
a) Fixed effects	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|	Value	95% CI	df	p>|t|
Intercept	4.49	2.28,6.68	31	0	4.31	2.16,6.45	31	<0.01	0.95	-1.92,3.83	31	0.50	0.73	-1.44,2.90	31	0.50
Region middle vs. east	2.36	-1,5.72	2	0.09	2.01	-1.23,5.25	2	<0.01	3.37	-2.41,9.15	2	0.12	1.44	-2.12,4.99	2	0.22
Region west vs. east	1.25	-2.32,4.83	2	0.27	1.72	-1.73,5.18	2	0.16	1.81	-4.10,7.72	2	0.31	0.56	-3.19,4.30	2	0.58
Reindeer density low vs. high	1.00	-1.81,3.82	2	0.26	0.31	-2.41,3.04	2	0.66	1.40	-3.36,6.16	2	0.33	0.50	-2.46,3.45	2	0.54
Moss layer	-0.30	-1.31,0.71	31	0.54	-1.27	-2.25, -0.28	31	0.01	-1.35	-2.36, -0.34	31	0.01	-0.28	-0.64,1.19	31	0.54
Litter cover	-0.91	-1.48, -0.34	31	<0.01	-0.07	-0.63,0.48	31	0.79	0.36	-0.23,0.95	31	0.22	-0.03	-0.57,0.51	31	0.90
b) Random effects																
~1|district			No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6				No. Obs.=70 No. Gr.=6	
St. Deviation (Intercept)	0.04				0.02				1.11				0.52			
~1|block			No. Gr.=37				No. Gr.=37				No. Gr.=37				No. Gr.=37	
St. Deviation (Intercept)	1.12				1.06				0.94				0.25			
Residuals	2.20	1.70,2.83			2.15	1.71,2.69			2.26	1.77,2.87			2.20	1.74,2.77		

DISCUSSION

The relationship of species' life history traits with the environment is an important determinant of successful reproduction (Chambers and MacHahon 1994, Fenner and Thompson 2005). The results from this study showed that both high and low reindeer density areas had a similar richness and abundance of life forms, growth forms, seed dispersal morphologies, and seed weight. This suggests that 20 years of contrasting reindeer densities are not important for the seed bank trait composition. Nevertheless, not all traits were evenly distributed in the seed bank. It is worth noting that a similar bias in the abundance of life history traits as that found in this study, has previously been linked to moderate and/or high grazing ecosystems (McNaughton 1984, McNaughton 1985, O´Connor and Pickett 1992, McIntyre et al. 1995, Post and Klein 1996). In addition, Finnmark has a long history of grazing, i.e. since the last ice age (Danell et al. 1999) and semi-domesticated reindeer have been managed since the 16th century (Muga 1986). In combination, this could suggest that the seed bank plant traits found in this study could reflect a general seed bank pattern of a long term grazed ecosystem.

Moen & Danell (2003) have claimed that the actual reindeer management strategy in Finnmark is unsustainable for the ecosystem. Furthermore, recent studies have already suggested that a decrease in reindeer densities could benefit both the vegetation (Bråthen et al. unpublished) and the reindeer fitness (Fauchald et al. 2004). From the present study it is only possible to suggest that, based on the seed bank trait pattern, the contrasted reindeer densities used in this study are similar.

Concerning the study design, because the required difference in reindeer densities between districts was only found in three pairs of districts, the design could lack the statistical power to detect the differences between high and low animal densities. Therefore, the absence of an effect of contrasting reindeer densities in this study should be interpreted with care. However, in spite of the low statistical power reported in the model, regional differences are statistically significant,

which suggests that a regional component in addition to the long term history of grazing could be more essential for explaining seed bank densities than the contrasting reindeer densities.

In light of the results, two temporal scales will be used in this discussion. These are the last 20 years of contrasting reindeer density, termed *short-term grazing history*, and the grazing that has taken place during centuries in Finnmark, referred to as *long-term grazing history*. Furthermore, the focus of the discussion will be the overall effects of grazing on the plant seed bank traits investigated and why they could reflect a general vegetation response pattern to a long history of grazing.

1. Total seed bank density and species richness

The seed bank densities in this study were higher than expected for alpine areas of the Fennoscandian subarctic region (Diemer and Prock 1993, Molau and Larsson 2000, Welling et al. 2004), finding them more in accordance with European alpine areas (Chambers 1995, Diemer and Prock 1993). However, this might be explained partly by the topography of the study areas. Concave curvature tends to accumulate snow and have a higher water run-off. In arctic and alpine environments, seeds tend to accumulate in the snow during late autumn and winter (Larsson and Molau 2001), what could make these concave areas appropriate for seed accumulation.

Moreover, the germinating conditions for the seeds at the phytotron used in this study were the most favourable the majority of alpine species could have, which could explain why so many seeds germinated compared to other studies. In the field, however, varying rates of recruitment depending upon species history traits, growing season conditions, and disturbance can be expected (Chambers 1995). Nevertheless, the seed densities in this study could be higher were we to look at the total viable seed bank, which includes those seeds that did not germinate during the germination period but still are alive and potentially capable of germination. Indeed, some studies have found a different seed density when comparing germinable vs. viable seed bank (Morin and Payette 1987). However, to check the viable seed bank, seeds must be sieved from

the soil and opened to check that the seed embryo is alive, which was beyond the scope of the project reported here.

The regional trend that is observed in the results could be attributed to a series of factors that we assumed to be included in the variable region. Slope, altitude and bedrock presented regional differences suggesting that a combination of these or other factors could be influencing the seed bank densities. The middle region seemed to have very high densities of seeds in comparison to the other two regions. A possible explanation could be that this region had higher mean temperature and precipitation than the normal in summer 2003 and 2004 (Meteorologisk.Institut 2006) (Table 3). Although not tested for in this study, climate is an important factor shaping alpine environments. It has been registered that small increases in temperature can accelerate flowering of some alpine species (Arroyo et al. 1981, Molau et al. 2005), which could increase seed production and consequently increase seed bank densities. Indeed, a higher flowering rate was recorded in the middle region (Ravolainen et al. unpublished) suggesting a climatic component could explain the elevated seed densities in this area.

Contrary to the findings of Tilman (1993) and Jutila (1998), litter cover did not reduce seed bank densities in this study. Instead the main inhibiting factor was the moss layer thickness. This suggests that the moss layer could have similar effects to litter cover in creating a mechanical barrier and impeding the incorporation of seeds into the seed bank, exposing them maybe to predation (Zamfir 2000) or making them germinate immediately once fallen to the ground.

2. Traits in the seed bank

2.1 Growth form

Although not influenced by short term grazing history, graminoids were the most successful growth form present in the studied seed bank. This growth form is known to be favoured by grazing (McNaughton 1984, Mulder 1999). Post & Klein (1996) found caribou in Alaska to enhance graminoid growth by adding nutrients to the soil through faeces and urine. The sampled

areas in the present study were assumed to be the ones reindeer visited most. Therefore, in addition to urine and faeces, trampling and grazing could also favour graminoid growth by reducing the abundance of dwarf shrubs and mosses, and by increasing temperature and nutrient turnover (van der Wal et al. 2001, Olofsson et al. 2004, van der Wal and Brooker 2004). The negative effect of moss layer on the abundance of graminoid seeds found in this study is consistent with this pattern, suggesting graminoid seed accumulation increases as moss layer decreases. Graminoids are usually more tolerant to grazing than dicotyledons (Hülber et al. 2005), which were the least abundant growth form in the seed bank .

While graminoids have inconspicuous and wind pollinated flowers, dicotyledon flowers in alpine areas are usually colorful in order to attract pollinators (Totland 2001). On the other hand, this could also attract grazers (Ehrlén 1997, Wada 1999, Cooper and Wookey 2003, Hülber et al. 2005). Since dicotyledons are the least abundant growth form in the studied seed bank, it seems that under grazing, the strategy of most dicotyledons of having colorful and large flowers does not seem to pay off. On the other hand, their seed bank species richness is similar to graminoids and three times higher than shrubs because it seems like many different species of dicotyledons are able to produce seeds.

In the sampled seed banks, shrubs/ericoids were the second in abundance much due to the presence of E*mpetrum nigrum spp hermafroditum* and *Vaccinium* genus. However, it is possible that ericoid shrubs could be more abundant because many unidentified seedlings probably belonged to *Empetrum* or *Vaccinium* genus. Many of these seedlings did not grow more than one centimeter during the whole germination period before dying. It is known that some ericoids require the presence of mycorrhiza in the soil in order to pick up nutrients (Tybirk et al. 2000). These mycorrhizas were most likely lacking from the soil at the phytotron, which could have impeded their growth. Furthermore, ericoid shrubs are not preferred by herbivores although ungulates eat their fruits (Bell and Tallis 1973). This pre-dispersal predation could allow for long distance dispersal of ericoid shrubs, allowing them to expand and exploit new locations. E*mpetrum* is known to have allelopatic substances in its growing leaves and litter cover that are even toxic to its own offspring and could even penetrate the soil. This could have inhibited the

germination rates in our study in those top layer samples where E*mpetrum* litter was collected or in the soil cores under E*mpetrum* individuals.

2.2 Life form

Hemicryptophyte and geophyte life forms are rather tolerant to grazing as their perennating buds are at or under the ground level and are thereforef abundant in the seed bank. Furthermore, the presented results suggest that the capacity of the other life forms than hemicriptophytes and geophytes to accumulate seeds could be reduced, maybe because other life forms have bigger seeds that germinate at once or do not enter the seed bank. Grazing has been found to promote prostrate hemicryptophytes over tall vegetation in reindeer exclusion studies (Virtanen et al.1997). This could suggest that from the long grazing history point of view, reindeer trampling and grazing in the studied areas could have favored hemicryptophytes and geophytes.

2.3 Diaspore morphology

Unappendaged diaspores were the most abundant in the seed banks. This diaspore morphology is most common in disturbed communities where the creation of microsites and liberation from competition by grazers is frequent (Venable and Brown 1988). These results could support the hypothesis that in environments where seed production has a dominating influence on effective dispersal, it will not pay off to have dispersal features (Eriksson and Jakobson 2000). This is because the advantage of evolving dispersal structures will not compensate for the costs in terms of fecundity, and a consequent trade off between seed size (including appendages) and seed number comes into play (Henery and Westoby 2001).

The results show the soil seed bank to contain more species with unappendaged diaspores than the top layer. This suggests that appendaged diaspores are less likely to enter the soil seed bank and therefore, are more prone to germinate soon after they land on the surface (Peart 1984) or to be eaten by predators (Rabinowitz 1981, Peart 1984). However, moss layer thickness has a strong negative effect on seed densities of all diaspore morphologies, which reinforces the importance of the mechanical barrier created by the moss layer.

Very few wind dispersed seeds germinated in this study. Those that did, mostly belonged to *Betula nana*, a species that is known to be sparse in seed banks and has a long distance dispersal capacity (Molau and Larsson 2000). This suggests long distance dispersal could mainly take place by animals. Indeed animal dispersed diaspores are more common than in the seed bank.

2.4 Seed mass

The results showed an abundance of small seeds (0-0.5mg) independent of the short term grazing history. This suggests that in the studied habitats that are partly covered by perennial vegetation and partly open as a result of periodic disturbance by reindeer, small-seeded plants manage to accumulate more seeds in the seed bank increasing their recruitment opportunities (Chambers et al. 1990, Chambers 1995). The results support also that small seeded species are able to build up large seed banks in the soil, as they are more capable of entering the soil than larger seeds (Thompson et al. 1997). Furthermore, small seeds face greater problems emerging in the field after deep burial and therefore often evolved a light requirement-form germination, which, as a by-product, leads to a long-lived seed bank (de Jong and Klinkhamer 2005). Litter cover was found to decrease the density of small size seeds (0-1 mg) in the seed bank. This is probably because they do not have enough accumulated reserves to grow through it (Venable and Brown 1988). It has also been hypothesized that large herbivores disperse small seeds, by ingesting them together with the vegetative plant parts by accident as they graze (Janzen 1984). The hypothesis was tested and confirmed by Myers et al. (2004) in a study with white-tailed deer. Although not considered an adaptation to animal presence, it could help to maintain an abundance of small seeds that apparently have no specific form of dispersal, by sparing them the need to develop appendages, allowing the parent plant to produce more seeds.

Intermediate size seeds (0.5-1 mg) have a better ability to emerge from deep burial in contrast to small seeds and are therefore also capable of forming a seed bank. Large seeds are nearly absent from the seed bank suggesting they germinate at once after falling or they are taken

by predators (Venable and Brown 1988, Eriksson and Jakobson 2000). Seed size should modify how natural selection shapes the physiological capacities of seedlings (Westoby et al. 1992). The evolution of seed size in a plant lineage has been closely linked to the evolution of many other plant traits, like longevity (larger seeds in longer-lived species), growth form (larger seeds in taller species) and dispersal mode (larger seeds are dispersed over shorter distances) (Venable and Brown 1988).

CONCLUSIONS AND FUTURE DIRECTIONS

Contrary to the study's hypothesis, the 20 years of contrasting reindeer densities did not affect the seed densities or the abundance of plant traits in the seed banks. As predicted, moss layer thickness had a negative effect on seed bank densities, while against the expectations litter cover only had a negative effect on small seed size (0-0.1 mg).

Although the link between the actual reindeer density in Finnmark and seed banks was not found, some patterns were detected concerning life history strategies. Independent of reindeer density, graminoids and hemicryptophytes were the more abundant plant traits, while small and unappendaged seeds were registered as the most successful seed traits. This combination of traits has been repeatedly implied to be a possible adaptation to grazing, suggesting that the long history of grazing of Finnmark (i.e. since the last ice age) could be one of the most important factors shaping the traits in the seed banks. Nevertheless, the model in this study shows a lot of variability explained by the region variable, suggesting that another factor as, e.g. climate, bedrock or topography, has an important effect on seed bank densities in addition to the long term history of grazing hypothesized here.

Today, the greatest challenge is to link the patterns found in the different studies to the mechanisms underlying them. The understanding of these mechanisms is what will facilitate generalization and prediction of vegetation response to environmental changes. This study has tried to link the life history traits present in the seed bank trait, to the grazing conditions of the ecosystem. The next step would be to find how life history traits in the seed bank are interconnected in relation to grazing.

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APPENDIX 1

Classification of identified species in the seed bank after the selected traits. References numbers as follows: 1=Biolflor internet data base; 2=Marianne Evju (pers.comm); 3=Thompson et al. 1997; 4=Grime et al. 1988; 5=Welling & Laine 2002; 6=My personal observation at Tromsø University Museum; 7=Welling et al. 2004; 8= Lid & Lid 1994; 9=http://www.ecoflora.co.uk

SPECIES	FAMILY	GROWTH FORM	LIFE FORM	ref	DIASPORE MORPHOLOGY	ref	SEED WEIGHT	ref
Agrostis capillaris	Poaceae	graminoid	hemicryptophyte	1	no appendages	7	0-0.1 mg	1
Agrostis mertensii	Poaceae	graminoid	hemicryptophyte	1	no appendages	7	0-0.1 mg	7
Alchemilla alpina	Rosaceae	dicotyledon	chamaephyte	1	with awns/hooks	7	>0.1-0.5 mg	7
Antennaria dioica	Asteraceae	dicotyledon	hemicryptophyte	1	with pappus	7	0-0.1 mg	7
Anthoxanthum odoratum ssp alpinum	Poaceae	graminoid	hemicryptophyte	1	with awns/hooks	7	>0.1-0.5 mg	7
Betula nana	Betulaceae	shrub	chamaephyte	1	with wings/fringes	7	>0.1-0.5 mg	7
Betula pubescens coll.	Betulaceae	shrub	phanerophyte	1	with wings/fringes	9	0-0.1 mg	1
Bistorta vivipara	Polygonaceae	dicotyledon	hemicryptophyte	1	no appendages	8	>0.1-0.5 mg	6
Campanula rotundifolia coll.	Campanulaceae	dicotyledon	hemicryptophyte	1	with pappus	7	0-0.1 mg	7
Cardamine bellidifolia	Brassicaceae	dicotyledon	hemicryptophyte	9	no appendages	7	>0.1-0.5 mg	7
Carex atrata	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	6	>1-5 mg	1
Carex brunnescens	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	6	>0.5-1 mg	1
Carex canescens	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	6	>0.1-0.5 mg	1
Carex capillaris	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	6	>0.1-0.5 mg	1
Carex lachenalii	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	7	>0.1-0.5 mg	7
Carex lachenalii x brunescens	Cyperaceae	graminoid	hemicryptophyte	1	na		na	
Carex norvegica ssp norvegica	Cyperaceae	graminoid	hemicryptophyte	1	no appendages	6	>0.1-0.5 mg	6
Carex sp	Cyperaceae	graminoid	hemicryptophyte	1	na		na	
Cerastium cerastoides	Caryophillaceae	dicotyledon	chamaephyte	9	no appendages	7	0-0.1 mg	7
Cerastium fontanum ssp fontanum	Caryophillaceae	dicotyledon	chamaephyte	9	no appendages	7	0-0.1 mg	7
Deschampsia cespitosa	Poaceae	graminoid	hemicryptophyte	1	with awns/hooks	9	>0.1-0.5 mg	1
Deschampsia flexuosa	Poaceae	graminoid	hemicryptophyte	1	with awns/hooks	7	>0.1-0.5 mg	1
Dicotyledon	na	na	na		na		na	
Empetrum nigrum ssp hermaphroditum	Empetraceae	shrub	chamaephyte	1	fleshy fruits	7	>1-5 mg	7
Epilobium anagallidifolium	Onagraceae	dicotyledon	chamaephyte	1	with pappus	8	0-0.1 mg	1
Epilobium hornemannii	Onagraceae	dicotyledon	chamaephyte	9	with pappus	8	0-0.1 mg	6
Epilobium lactiflorum	Onagraceae	dicotyledon	chamaephyte	9	with pappus	8	0-0.1 mg	9
Epilobium montanum	Onagraceae	dicotyledon	chamaephyte	9	with pappus	8	>0.1-0.5 mg	9
Ericoid	na	na	na		na		na	
Festuca rubra coll.	Poaceae	graminoid	hemicryptophyte	1	with awns/hooks	9	>1-5 mg	1
dicotyledon	na	na	na		na		na	
Hieracium alpina nigrescantia	Asteraceae	dicotyledon	hemicryptophyte	1	with pappus	7	>0.1-0.5 mg	7

Juncus filiformis	Juncaceae	graminoid	hemicryptophyte|9	no appendages|9	>0.1-0.5 mg|9
Juncus trifidus	Juncaceae	graminoid	hemicryptophyte|1	no appendages|7	0-0.1 mg|1
Leontodon autumnalis	Asteraceae	dicotyledon	hemicryptophyte|1	with pappus|9	>0.5-1 mg|1
Luzula arcuata coll.	Juncaceae	graminoid	hemicryptophyte|1	no appendages|8	>0.1-0.5 mg|1
Luzula multiflora coll.	Juncaceae	graminoid	hemicryptophyte|1	elaisome|2	>0.1-0.5 mg|1
Luzula pilosa	Juncaceae	graminoid	hemicryptophyte|1	elaisome|8	>0.1-0.5 mg|6
Luzula sudetica	Juncaceae	graminoid	hemicryptophyte|1	with awns/hooks|8	>0.1-0.5 mg|1
Monocotyledon	Na	na	na	na	na	na
Nardus stricta	Poaceae	graminoid	hemicryptophyte|1	with awns/hooks|7	>0.5-1 mg|1
Omalotheca norvegica	Asteraceae	dicotyledon	hemicryptophyte|9	with pappus|3	0-0.1 mg|6
Omalotheca supina	Asteraceae	dicotyledon	hemicryptophyte|9	with pappus|3	0-0.1 mg|6
Oxyria digyna	Polygonaceae	dicotyledon	hemicryptophyte|1	with wings/fringes|7	>0.5-1 mg|7
Phleum alpinum	Poaceae	graminoid	hemicryptophyte|1	with awns/hooks|7	>0.1-0.5 mg|1
Plant	na	na	na	na	na
Poa alpina coll.	Poaceae	graminoid	hemicryptophyte|1	with awns/hooks|7	>0.1-0.5 mg|1
Poa glauca coll.	Poaceae	graminoid	hemicryptophyte|1	with awns/hooks|5	>0.1-0.5 mg|6
Poa pratensis ssp alpigena	Poaceae	graminoid	hemicryptophyte|1	no appendages|7	>0.1-0.5 mg|1
Potentilla crantzii	Rosaceae	dicotyledon	hemicryptophyte|1	no appendages|7	>0.5-1 mg|7
Ranunculus acris coll.	Ranunculaceae	dicotyledon	geophyte|1	with awns/hooks|7	>1-5 mg|7
Ranunculus pygmaeus	Ranunculaceae	dicotyledon	geophyte|1	with awns/hooks|7	0-0.1 mg|1
Rumex acetosa coll.	Polygonaceae	dicotyledon	hemicryptophyte|1	no appendages|7	>0.5-1 mg|7
Sagina saginoides	Caryophillaceae	dicotyledon	chamaephyte|9	no appendages|6	0-0.1 mg|6
Salix herbacea	Salicaceae	shrub	phanerophyte|1	with pappus|7	0-0.1 mg|7
Salix reticulata	Salicaceae	shrub	phanerophyte|1	with pappus|7	0-0.1 mg|1
Saxifraga rivularis	Saxifragaceae	dicotyledon	chamaephyte|1	no appendages|6	0-0.1 mg|6
Saxifraga stellaris	Saxifragaceae	dicotyledon	chamaephyte|1	no appendages|6	>0.5-1 mg|1
Sibbaldia procumbens	Rosaceae	dicotyledon	hemicryptophyte|1	no appendages|7	>0.1-0.5 mg|7
Taraxacum sp	Taraxaceae	dicotyledon	hemicryptophyte|8	with pappus|7	>0.1-0.5 mg|7
Trisetum spicatum	Poaceae	dicotyledon	hemicryptophyte|1	no appendages|6	>0.1-0.5 mg|7
Vaccinium myrtillus	Ericacea	shrub	chamaephyte|1	fleshy fruits|7	>0.1-0.5 mg|7
Vaccinium uliginosum	Ericacea	shrub	chamaephyte|1	fleshy fruits|9	>0.1-0.5 mg|1
Vaccinium vitis-idaea	Ericacea	shrub	chamaephyte|1	fleshy fruits|7	>0.1-0.5 mg|7
Veronica alpina ssp alpina	Scrophulariacea	dicotyledon	chamaephyte|9	no appendages|7	0-0.1 mg|7
Viola biflora	Violaceae	dicotyledon	hemicryptophyte|1	no appendages|7	>0.1-0.5 mg|7
Viola palustris	Violaceae	dicotyledon	hemicryptophyte|1	elaisome|2	>0.5-1 mg|9

APPENDIX 2

Mean seed densities m^2 in the different districts, including in parenthesis minimum and maximum mean seed density encountered in the study areas.

REGION	District ID Reindeer density	Soil Mean seeds/m^2	Top layer Mean seeds/m^2	Total Germinable Mean seeds/m^2
East	27 High density	109 (0- 3061)	339 (0- 2166)	575 (0- 2284)
	28 Low density	701 (0- 3741)	540 (133- 1114)	1202 (221- 5869)
Middle	20 High density	1830 (0-9439)	588 (0-1745)	3506 (0- 12930)
	21 Low density	1885 (0-7653)	968 (0-2056)	2854 (221- 12774)
West	6 High density	672 (0-6327)	237 (0-997)	864 (0-6805)
	7 Low density	275 (0-1020)	341 (0-931)	588 (0-2563)
TOTAL	HIGH DENSITY	1223	556	1648
	LOW DENSITY	1009	596	1528

APPENDIX 3

Species mean seed density per district. The species are presented in order of abundance after the mean of total high and total low reindeer density areas (**in bold**)

SPECIES	DISTRICT 6	20	27	TOTAL HIGH	SPECIES	DISTRICT 7	21	28	TOTAL LOW
Plant	447.66	2595.3	189.6	**1077.52**	*Carex brunnescens*	0	2312.3	463.74	**925.35**
Carex brunnescens	778.88	171.37	7.38	**319.21**	Plant	35.44	1535.27	466.7	**679.14**
Dicotyledon	3.92	377.25	109.44	**163.54**	*Cerastium cerastoides*	6.65	510.25	2.21	**173.04**
Carex lachenalii	300.91	140.9	23.02	**154.94**	*Carex lachenalii*	56.52	369.81	41	**155.78**
Vaccinium myrtillus	3.3	21.26	264.77	**96.44**	*Sagina saginoides*	10.64	255.13	0	**88.59**
Empetrum nigrum ssp hermaphroditum	5.32	105.21	74.87	**61.80**	*Betula nana*	222.05	16.31	0	**79.45**
Nardus stricta	0.83	170.21	0	**57.01**	*Vaccinium myrtillus*	5.98	24.98	184.72	**71.89**
Agrostis mertensii	0.83	122.25	17.54	**46.87**	*Sibbaldia procumbens*	18.62	6.15	180.79	**68.52**
Deschampsia flexuosa	129.22	2.21	6.3	**45.91**	*Saxifraga rivularis*	0	0	204.1	**68.03**
Epilobium hornemannii	1.66	102.16	6.92	**36.91**	*Carex canescens*	0	170.08	1.84	**57.31**
Ericoid	0	28.8	62.01	**30.27**	*Agrostis mertensii*	6.93	52.01	41.93	**33.62**
Graminoid	41.5	36.44	9.56	**29.17**	*Epilobium hornemannii*	29.26	34.17	32.51	**31.98**
Omalotheca supina	1.66	28.07	6.46	**12.06**	*Nardus stricta*	0	80.25	14.77	**31.67**
Deschampsia cespitosa	0	18.01	14.25	**10.75**	*Empetrum nigrum ssp hermaphroditum*	15.5	45.2	18.84	**26.51**
Betula nana	20.77	0	5.54	**8.77**	Ericoid	3.32	62.13	3.69	**23.05**
Leontodon autumnalis	0	23.55	0	**7.85**	Dicotyledon	9.31	49.9	7.2	**22.14**
Salix herbacea	17.45	4.35	0	**7.27**	Graminoid	10.54	30.77	21.61	**20.97**
Anthoxanthum odoratum ssp alpinum	0	17.08	3.69	**6.92**	*Juncus filiformis*	0	45.52	0	**15.17**
Sibbaldia procumbens	0	12.19	4.15	**5.45**	*Omalotheca supina*	14.25	11.49	19.02	**14.92**
Sagina saginoides	3.32	6.92	4.15	**4.80**	*Salix herbacea*	10.26	25.72	5.54	**13.84**
Monocotyledon	3.46	10.25	0	**4.57**	*Anthoxanthum odoratum ssp alpinum*	8.64	19.13	10.71	**12.83**
Luzula multiflora coll.	2.07	11.08	0	**4.38**	*Veronica alpina ssp alpina*	2.66	0	28.44	**10.37**
Vaccinium uliginosum	0	0	12.66	**4.22**	*Carex norvegica ssp norvegica*	0	22.62	7.38	**10.00**
Carex lachenalii X brunescens	5.19	4.98	1.84	**4.00**	*Deschampsia flexuosa*	0	15.75	12.74	**9.50**
Bistorta vivipara	0	11.08	0	**3.69**	*Alchemilla alpina*	2.66	0	14.77	**5.81**
Veronica alpina ssp alpina	0	1.38	9.23	**3.54**	*Rumex acetosa coll.*	0	4.35	10.71	**5.02**
Juncus trifidus	1.03	5.18	3.69	**3.30**	*Carex lachenalii X brunescens*	7.6	0	5.35	**4.32**
Vaccinium vitis.idaea	0	0	9.5	**3.17**	*Phleum alpinum*	0	2.77	9.79	**4.19**
Rumex acetosa coll.	1.87	6.92	0	**2.93**	*Carex atrata*	8.55	3.69	0	**4.08**
Carex norvegica ssp norvegica	0	1.38	5.54	**2.31**	*Luzula multiflora coll.*	0	11.08	0	**3.69**
Phleum alpinum	0	6.92	0	**2.31**	Monocotyledon	0	7.38	3.69	**3.69**
Ranunculus acris coll.	6.65	0	0	**2.22**	*Trisetum spicatum*	7.98	1.58	0	**3.19**
Poa pratensis ssp alpigena	0	0	5.93	**1.98**	*Omalotheca norvegica*	6.65	1.84	0	**2.83**
Betula pubescens coll.	0.83	0	3.69	**1.51**	*Luzula sudetica*	2.66	5.54	0	**2.73**
Saxifraga rivularis	0	4.43	0	**1.48**	*Ranunculus pygmaeus*	0	0	8.12	**2.71**
Campanula rotundifolia coll.	0	0	3.16	**1.05**	*Saxifraga stellaris*	0	5.54	2.21	**2.58**
Cardamine bellidifolia	0	0	2.77	**0.92**	*Luzula pilosa*	0	7.38	0	**2.46**
Festuca rubra coll.	0	2.7	0	**0.90**	*Juncus trifidus*	0	4.66	2.21	**2.29**
Cerastium cerastoides	0.83	1.38	0	**0.74**	*Taraxacum sp*	0	2.77	3.69	**2.15**

Species					Species				
Epilobium lactiflorum	0.83	1.38	0	**0.74**	Viola biflora	5.98	0	0	**1.99**
Luzula arcuata coll.	0	2.21	0	**0.74**	Bistorta vivipara	0	2.77	2.77	**1.85**
Saxifraga stellaris	1.66	0	0	**0.55**	Vaccinium uliginosum	0	4.61	0	**1.54**
Viola palustris	0	1.58	0	**0.53**	Deschampsia cespitosa	2.66	0	1.84	**1.50**
Antennaria dioica	0	1.38	0	**0.46**	Hieracium alpina nigrescantia	0	2.77	0.92	**1.23**
Carex atrata	0	1.38	0	**0.46**	Oxyria digyna	0	3.69	0	**1.23**
Carex sp	0	1.38	0	**0.46**	Vaccinium vitis.idaea	0	3.28	0	**1.09**
Epilobium anagallidifolium	0	1.38	0	**0.46**	Epilobium montanum	2.66	0	0	**0.89**
Omalotheca norvegica	0	1.38	0	**0.46**	Salix reticulata	2.66	0	0	**0.89**
Poa alpina coll.	0	1.38	0	**0.46**	Agrostis capillaris	0	0	2.21	**0.74**
Poa glauca coll.	0	0	1.38	**0.46**	Carex capillaris	0	0	2.21	**0.74**
Taraxacum sp	0	1.38	0	**0.46**	Potentilla crantzii	0	0	2.21	**0.74**
Trisetum spicatum	0	0	1.38	**0.46**	Epilobium anagallidifolium	0	1.87	0	**0.62**
Agrostis capillaris	0	0	0	**0**	Leontodon autumnalis	0	0	1.84	**0.61**
Alchemilla alpina	0	0	0	**0**	Ranunculus acris coll.	0	0	1.84	**0.61**
Carex canescens	0	0	0	**0**	Luzula arcuata coll.	0	1.84	0	**0.61**
Carex capillaris	0	0	0	**0**	Cerastium fontanum ssp fontanum	0	1.84	0	**0.61**
Cerastium fontanum ssp fontanum	0	0	0	**0**	Poa pratensis ssp alpigena	0	0	0	**0**
Epilobium montanum	0	0	0	**0**	Betula pubescens coll.	0	0	0.	
Hieracium alpina nigrescantia	0	0	0	**0**	Campanula rotundifolia coll.	0	0	0	**0**
Juncus filiformis	0	0	0	**0**	Cardamine bellidifolia	0	0	0	**0**
Luzula pilosa	0	0	0	**0**	Festuca rubra coll.	0	0	0	**0**
Luzula sudetica	0	0	0	**0**	Epilobium lactiflorum	0	0	0	**0**
Oxyria digyna	0	0	0	**0**	Viola palustris	0	0	0	**0**
Potentilla crantzii	0	0	0	**0**	Antennaria dioica	0	0	0	**0**
Ranunculus pygmaeus	0	0	0	**0**	Carex sp	0	0	0	**0**
Salix reticulata	0	0	0	**0**	Poa alpina coll.	0	0	0	**0**
Viola biflora	0	0	0	**0**	Poa glauca coll.	0	0	0	**0**

APPENDIX 4

Seed bank information table. (1) Mean seed density (seeds/m^2) in the seed bank for each trait in the different districts; (2) The minimum and maximum mean seed densities per study area for each district; and (3) the mean species richness for each trait per district or reindeer density.

		REGION																		TOTAL			
		East						Middle						West									
		Reindeer density (district ID)						Reindeer density (district ID)						Reindeer density (district ID)									
		High (6)			Low (7)			High (20)			Low (21)			High (27)			Low (28)			HIGH		LOW	
TRAITS		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	3	1	3
GROWTH FORM	Graminoid	246	(0-2994)	0,43	287	(0-1453)	0,57	1495	(0-7514)	2,6	1369	(0-4983)	2,23	167	(0-676)	0,63	470	(0-1720)	1,25	636	1,2	709	1,4
	Dicotyledon	18	(0-186)	0,12	108	(0-638)	0,59	309	(0-1210)	0,92	237	(0-1697)	0,52	38	(0-232)	0,24	349	(0-1561)	0,76	122	0,4	231	0,6
	Shrub	494	(0-3203)	0,30	93	(0-541)	0,36	168	(0-765)	0,15	162	(0-354)	0,57	371	(0-1742)	0,42	239	(0-1789)	0,3	344	0,3	165	0,4
LIFE FORM	Phanerophyte	439	(0-6367)	0,09	13	(0-66)	0,01	3	(0-33)	0,03	26	(0-233)	0,06	3	(0-44)	0,027	47	(0-204)	0,05	148	0,1	28	0,4
	Chamaephyte	63	(0-301)	0,26	135	(0-350)	0,56	349	(0-1846)	0,39	307	(0-543)	0,75	387	(0-340)	0,52	452	(66-1279)	0,61	266	0,4	298	0,6
	Hemicryptophyte	256	(0-3011)	0,49	341	(0-1452)	0,9	1619	(0-8035)	3,25	1435	(0-7130)	2,52	207	(0-776)	1,5	559	(44-1827)	1,57	694	1,5	778	1,7
DIASPORE MORPHOLOGY	No appendages	228	(0-2672)	0,41	226	(0-502)	0,68	1398	(0-8579)	1,68	1282	(0-5267)	1,68	184	(0-378)	0,6	600	(0-1064)	1,21	604	1	703	1,2
	pappus	442	(0-6354)	0,11	66	(0-166)	0,33	182	(0-984)	0,61	109	(0-510)	0,34	16	(0-116)	0,09	186	(0-1437)	0,35	214	0,3	120	0,3
	hooks	25	(0-255)	0,06	57	(0-434)	0,14	212	(0-909)	0,83	189	(0-842)	0,65	25	(0-66)	0,26	74	(0-155)	0,46	88	0,4	107	0,4
	fruits	34	(0-228)	0,07	21	(0-99)	0,13	164	(0-1530)	0,12	120	(0-543)	0,42	361	(0-1742)	0,35	200	(0-1723)	0,24	187	0,2	114	0,3
	wings	21	(0-72)	0,14	59	(0-488)	0,15	0	0	0	20	(0-110)	0,11	9	(0-66)	0,069	7	(0-44)	0,02	4	0,02	4	0.02
	elaisome	2	(0-33)	0,02	0	0		9	(0-133)	0,05	18	(0-133)	0,09	0	0	0	7	(0-44)	0,02	4	0,02	8	0.02
SEED WEIGHT	0-0,1 mg	421	(0-6327)	0,02	0	0		297	(0-3571)	0,98	286	(0-1530)	0,66	21	(0-255)	0,38	186	(0-1224)	0,78	247	0,5	157	0,6
	0,1-0,5 mg	153	(0-642)	0,44	269	(0-909)	0,76	596	(0-1316)	1,32	346	(0-1442)	1,11	382	(0-1476)	0,71	332	(0-1767)	0,84	377	0,8	316	0,9
	0,5-1 mg	113	(0-882)	0,12	55	(0-204)	0,12	752	(0-5427)	1,19	882	(0-5910)	1,2	64	(0-340)	0,055	376	(0-1508)	0,53	310	0,5	438	0,6
	1-5 mg	37	(0-210)	0,08	15	(0-99)	0,09	152	(0-662)	0,13	91	(0-510)	0,32	74	(0-361)	0,14	24	(0-79)	0,12	88	0,1	43	0,2