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# The Effect of Restoration Treatments on the Regeneration Pathway in Alpine Seed Plants

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Biology

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## PREFACE

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## ABSTRACT

**Question:** How does nutrient addition and seeding affect revegetation of seed plants, and are the effects differing among the stages of the regeneration pathway?

**Location:** Two roads restored in 2002, located in Hjerkin firing range, in lower alpine zone of Dovrefjell, Norway.

**Methods:** Abundance of species and functional types (dwarf shrubs, forbs and graminoids) in four stages of the regeneration pathway (seed rain, seed bank, field seedlings and established vegetation) was recorded seven years after road reconstruction in treatment plots (with nutrient addition, nutrient + seed addition and no treatment).

**Results:** The graminoid *Deschampsia cespitosa* dominated the vegetation and seed rain in fertilized plots, while the seeded *Festuca rubra* still dominated the seeded + fertilized plots. The germinable seed bank was lowest in the seeded + fertilized treatment, while control plots had the highest number of seedlings in the field. Dwarf shrubs had a high germination rate in the field, despite low rates in the seed rain and seed bank. The highest rate of dwarf shrub seedlings was in control plots, while the frequency of dwarf shrubs in the established vegetation increased with nutrient addition. Forbs had species specific responses.

**Conclusions:** Both fertilized treatments were dominated by graminoids, with a higher vegetation cover and frequency of dwarf shrubs than the control plots. While graminoids are the most efficient seed producers, they are less able to establish seedlings. Dwarf shrubs accounted for a high proportion of germinating seedlings in the field, but the low frequencies of dwarf shrubs in the established control plot vegetation suggest either low seedling survival or an ongoing successional change. It remains to be revealed if the high recruitment of dwarf shrubs in the control plots will speed up the establishment of the typical dwarf shrub cover similar to the surrounding vegetation and hereby indicate that unassisted recovery is the fastest way to restore alpine dwarf shrub heath.

## SAMMENDRAG

**Spørsmål:** Hvordan påvirker tilsetning av næring og frø revegetering fra frøplanter, og er effektene ulike mellom stadiene i livssyklusen (Frøregn, frøbank, spirer i felt og etablert vegetasjon)

**Sted:** To veier restaurert i 2002, beliggende i Hjerkinns skytefelt, i den lågalpine sonen på Dovrefjell, Norge.

**Metoder:** Mengden arter og funksjonelle grupper (dvergbusker, urteplanter og gress) i fire stadier av livssyklusen ble observert i forsøksfelt, sju år etter restaureringen av veiene (med tilsatt næring, næring + frø og ingen behandling)

**Resultater:** Behandlingene påvirket alle stadier av livssyklusen. Gressarten *Deschampsia cespitosa* dominerte vegetasjonen og frøregnet i forsøksfeltene tilsatt næring, mens feltene tilsatt næring + frø fortsatt var dominert av den isådde *Festuca rubra*. Den spiredyktige frøbanken var lavest i feltene tilsatt næring + frø, mens kontrollfeltene hadde høyest antall spirer i felt av alle funksjonelle grupper. Dvergbuskene hadde høy spiringsrate i felt, til tross for lavt antall frø i frøregnet og spirer i frøbanken. Denne gruppen hadde høyest spiringsrate i kontrollfeltene, men frekvensen av etablerte dvergbusker var høyest der det var tilsatt næring. Urteplantene viste artsspesifikke responser.

**Konklusjoner:** Begge behandlingene som inkluderte næringstilsetning var dominert av gressarter sju år etter behandling, med et høyere vegetasjonsdekke og økt frekvens av dvergbusker i forhold til kontrollfeltene. Selv om gressartene produserer mest frø har de større vanskeligheter med å etablere seg som spirer i den etablerte vegetasjonen. Dvergbusker utgjorde en stor andel av spirene funnet i felt, men den lave frekvensen av dvergbusker i kontrollfeltenes etablerte vegetasjon tilsier enten lav overlevelse av spirer eller en pågående suksesjon der artssammensetningen i disse feltene er i endring. Det gjenstår å se om den høye rekrutteringen av dvergbusker i kontrollfeltene vil øke utviklingen mot det typiske dvergbuskdekket i den omkringliggende vegetasjonen, og dermed indikere at alpin dvergbuskhei restaureres best uten omfattende behandlinger.



## INTRODUCTION

Alpine and sub-alpine vegetation is considered to be structured by abiotic factors causing a short and intense growing season, low decomposition rates and great natural fluctuations in environmental conditions (Soudzilovskaia et al. 2005). The unpredictability of the alpine environment favors vegetative means of reproduction, which traditionally is considered the most common source of recruitment (Bell et al. 1980). Still, more recent studies from the alpine tundra show seedling establishment either within or above the range of perennial species from other environments (Forbis 2003, Schlag et al. 2000). Also for species that predominantly reproduce vegetative, sexual recruitment is important for maintaining genetic diversity within the population, and for vegetating previously unoccupied areas (Suding et al. 2004). Disturbance causes such gaps in vegetation, which is occupied either by pre-existing seed banks in the soil or dispersed propagules from adjacent vegetation (May et al. 1982). Large scale disturbances are primarily revegetated by seed producing plants, as they have potential for long distance dispersal and long term viability through seed bank dormancy (Gartner et al. 1983), and effective seedling establishment is therefore crucial for successful large scale restoration attempts.

For a plant individual to successfully establish at a given site, all stages of the regeneration pathway must be accomplished; seed set, seed dispersal, germination and seedling establishment and survival (Welling et al. 2002). Seed set in the alpine is assumed to be infrequent due to abiotic constraints (Chambers 1993), and results from seed addition experiments suggest that seed limitation is a main factor restricting plant species richness (Lindgren et al. 2007, Mayer et al. 2011, Myers et al. 2009). Seeds are often small and lack specialized adaptations for dispersal, or they are adapted to wind dispersal. Hence, their distribution is mainly influenced by wind and soil surface characteristics (Chambers et al. 1994). The cold soils promote seed longevity, but with few species in the ecosystem, the seed bank composition is mostly similar to the standing vegetation (Chambers 1993). It has also been suggested that availability of suitable microsites is the key factor governing recruitment patterns (Cichini et al. 2011, Graae et al. 2011), and there is evidence suggesting that the transition from seed pool to the phase of seedling emergence is more critical than the transition from seedling emergence to survived seedling (Chambers 1993, Clark et al. 2007). The complex interactions between recruitment filters may pose bottlenecks to successful establishment beyond that of each discrete factor (Garcia-Camacho et al. 2010).

Seedling mortality occur predominantly during the first year of life across diverse environments, and surviving this stage is an important threshold for successful seedling establishment (De Steven 1991, Gartner et al. 1983, Osburn 1961, Tanouchi et al. 1994). In environments characterized by extreme conditions such as the alpine, neighboring plants

may ameliorate the microclimate by improving resource availability or increasing soil moisture (Padilla et al. 2006). The relative importance of facilitation and competition are shown to vary along an environmental gradient, with competition dominating sheltered, high productive habitats, switching to facilitation as the habitat becomes more xeric and exposed, when for instance moving up to higher elevations in an alpine landscape (Choler et al. 2001).

Loss of habitat for both plants and animals is currently the predominant threat against biological diversity worldwide (Millenium Ecosystem Assessment 2005), and the level of anthropogenic activity is now escalating in arctic and alpine areas, inducing large scale disturbance pressures (Forbes et al. 2001). Several studies on alpine and arctic vegetation show low resistance towards anthropogenic disturbance, and also such low resilience that certain plant communities may not recover to their pre-disturbed state in the foreseeable future (Soudzilovskaia et al. 2007, Soudzilovskaia et al. 2006). Ecological restoration is defined as “*the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed*”. For both aesthetical and ecological purposes, restoration through assisted vegetation recovery may be used to achieve a vegetation cover resembling that of native surroundings, but the knowledge of restoration ecology in alpine regions are sparse compared to that of lowlands (Erschbamer et al. 2001). Three main procedures are used in arctic and alpine areas to improve the establishment of a vegetation cover following disturbance; seeding or planting of local species, nutrient addition and tillage and manipulation of the terrain (Hagen 2010, Urbanska et al. 1997).

Our aim has been to study how such restoration measures affect the regeneration pathway in newly restored alpine areas; if and how natural recovery by seeds differs between restoration treatments. To get a complete impression of the regeneration pathway we sampled data from four distinct phases of the pathway; seed rain, seed bank, seedling germination in the field and established vegetation. Adaptions to different stages of succession leads to species having very different life histories, and we separated between the growth forms dwarf shrubs, forbs and graminoids to investigate potential variation between these groups in response to the treatments. To identify possible species specific responses, we chose some native key species commonly found in the undisturbed vegetation, including both early succession (*Euphrasia* sp., *Rumex acetosella*, *Astragalus* sp., *Campanula rotundifolia*) and late succession (*Betula nana*, *Empetrum nigrum*) species, as well as two species of graminoids known to dominate after artificial nutrient addition and seeding (*Deschampsia cespitosa*, *Festuca rubra*). More specifically, our aims were to test:

(1) Does nutrient and seed addition lead to increased vegetation cover, with more seed production and entrapment?

(2) Does vegetation cover have a positive facilitative effect, with more germinating seedlings in more densely vegetated areas?

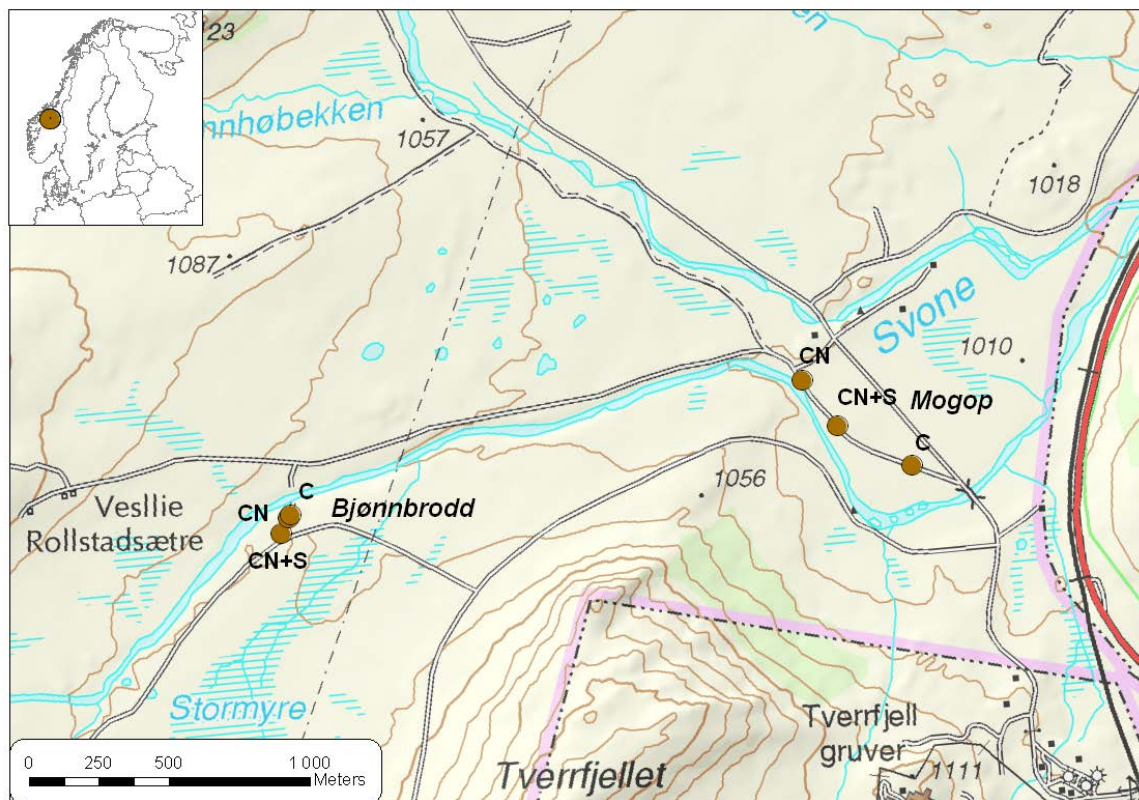
(3) Is the effect of treatment different among the three functional groups (dwarf shrubs, forbs and graminoids), and are species with divergent life histories affected in different stages of the regeneration pathway?



## METHODS

### STUDY SITE

The study site Hjerkinn is located at Dovrefjell mountain, Oppland county, Norway (Figure 1). Hjerkinn is situated in the more species poor western areas of Dovre, with our study sites found in the lower alpine zone 1000-1100 m a.s.l. The area is characterized by mean temperatures ranging from -8.8°C in January to 9.8°C in July and a mean annual precipitation of 435 mm (Norwegian Meteorological Institute 2011). The study area is dominated by glacial sediments which are coarse and poor in calcium (The Norwegian Institute for Soil and Forest Mapping 1999).



**Figure 1:** The study site, Hjerkinn. The two restored roads are named “Mogop” and “Bjønbrodd”, with C, CN and CN+S indicating the three different treatments in each area (Table 1 for details)

Hjerkinn firing range (165 km<sup>2</sup>) was established in 1923. In 1999 it was decided to seize all military activity, and the process to restore the area back to a natural state has now started (Martinsen et al. 2010). During July-August 2002 a pilot study was established to

examine the effect of different restoration procedures on 1,2 km removed roads in the firing range. The restored areas were divided into several treatment patches, and the long term results from this study are intended to draw guidelines for the restoration of the entire firing range (Hagen 2004). Our study includes two areas along the restored roads, both dominated by low growth heather and dwarf birch vegetation. The roads were restored with mechanical removal of all excess landfill, and subsequent loosening of the compressed original surface. In all studied areas, a mosaics of transplant turfs from surrounding vegetation with a size of less than 1m<sup>2</sup> and more than 10 m apart was placed across the restored roads, expected to both facilitate for new vegetation establishment, but also spread and produce new propagules themselves (Hagen 2004). A system of different treatment regimens was conducted, three of them examined in this study (Table 1).

**Table 1:** The three different treatment procedures included in this study, with code and description of each treatment

Name	Code	Description
Soil processing (Control)	C	Loosening of the compressed original surface, transplants from surrounding vegetation scattered across the area (Basic treatment in all fields).
Fertilization (Control + Nutrients)	CN	In addition to treatment C, the area is added NPK-fertilizer (20g/m <sup>2</sup> )
Alginate, fertilization and seeding (Control, Nutrients + Seeds)	CN+S	In addition to treatment CN, the soil is added a mixture of peat, alginate binder, water and commercial seeds of <i>Festuca rubra</i> ssp. <i>rubra</i> (10g/m <sup>2</sup> ).

## ESTABLISHED VEGETATION

The established vegetation was recorded in 2009 through square frame analyses (0.5m x 0.5m), with five plots randomly distributed within each treatment area (15 per test field, and a total of n=30). The frequency of all species was recorded (present/absent in 16 subplots within each plot). Also, a visual estimation of percentage vegetation cover was conducted for each plot, including the cover of bryophytes and lichens. With the restoration being initialized in 2002, most of the established vegetation at the time of survey was approximately 7 years old.

## SEED RAIN

Plastic AstroTurf™ doormat seed traps (0.2m x 0.5m) were used to measure all diaspore dispersal in to the study area. In remote areas with limited availability to check and empty the traps, this method is recognized to perform diaspore collection satisfactory (Larsson 2004). Twenty mats were evenly spread out over the same area where the seed bank samples were collected, adding up to 60 mats per test field and a total of 120 mats for the study. The mats were nailed to the ground in early June 2010, and left for the entire growing season. All mats were collected in separate plastic bags at the first day of snow in early October 2010, and placed indoors with the top of the bag open to dry without damaging from moisture and fungal attack. When dried, the mats were emptied of all contents. Contents from ten seed traps from each treatment and from both roads (n = 60), were examined individually with a stereo lens. The seeds were determined to the species or genus level whenever possible, otherwise recorded as unknown monocot or dicot, and counted.

## SEED BANK

The seed bank samples were collected during spring 2009, and represent the viable seeds which were produced in the previous growth season or earlier. Samples were collected as cylindrical cores with a diameter of 7 cm, and a depth of 2 cm. In each treatment 20 cores were sampled randomly from an area of 700 m<sup>2</sup>, adding up to 60 cores per test field and a total of 120 samples. The cores were separately bagged and frozen until January 2010. After a day of thaw, each sample was sifted for roots and large litter fragments, and sprinkled on top of commercial plant soil in open plastic boxes of 0.02 m<sup>2</sup>.

The containers were placed in the green house, with an ambient temperature of 18-20°C and 15 hours of daylight, which has been demonstrated to be optimum germination conditions for several arctic and alpine species (Alsos et al. 2003). Seedlings were recorded every third day, cultivated until the species could be determined and then removed to avoid competition with other seeds and seedlings. To maximize potential germination we stirred the top layer of soil after 4 weeks, to loosen bryophytes and crust and bring buried seeds to the surface. After 13 weeks in the greenhouse all containers were put in a refrigerator in 3°C for 3 weeks to simulate winter conditions. They were then put back into the greenhouse and new seedlings recorded for 10 weeks more. All seedlings that died before determination of species were recorded as unknown monocot or dicot.

## NATURALLY OCCURRING SEEDLINGS IN THE FIELD

All seedlings belonging to a size class indicating an age of 0-2 years were mapped through square frame analyses (0.5x0.5 m) in all treatment sites during august 2010. 20 plot analyses at each treatment, one plot adjacent to each seed trap (60 per test field and a total of n=120). All seedlings were counted and recorded to genus or species whenever this was possible, otherwise as unknown monocot or dicot.

## STATISTICS

In the statistical analyses the percentage cover of vascular plant species, frequency of each functional type in the established vegetation, number of seeds from traps, number of seedlings from the seed bank and number of seedlings found in the field were used. To compare the effect of different treatments and functional types in terms of vegetation cover, frequency in the established vegetation and number of seedlings found in the field, repeated measures of analyses of variance (ANOVA) was used. To fulfill the assumptions of normal distributions, the number of field seedlings and seeds in the seed rain were log-transformed. We found an interaction with study area in the seed rain data, and therefore chose to analyze the number of seeds as a function of treatment with a linear mixed effect model (LME). The number of seedlings germinating from the seed bank showed a clear misfit to linear models, and was therefore log-transformed and analyzed with a generalized linear model (GLM) with negative binomial error structure. A result is termed statistically significant if it is unlikely to have occurred by chance, measured as a critical p-value  $\leq 0.05$ . All statistical analyses was performed with the R software, version 2.13.2 (R Development Core Team 2011).

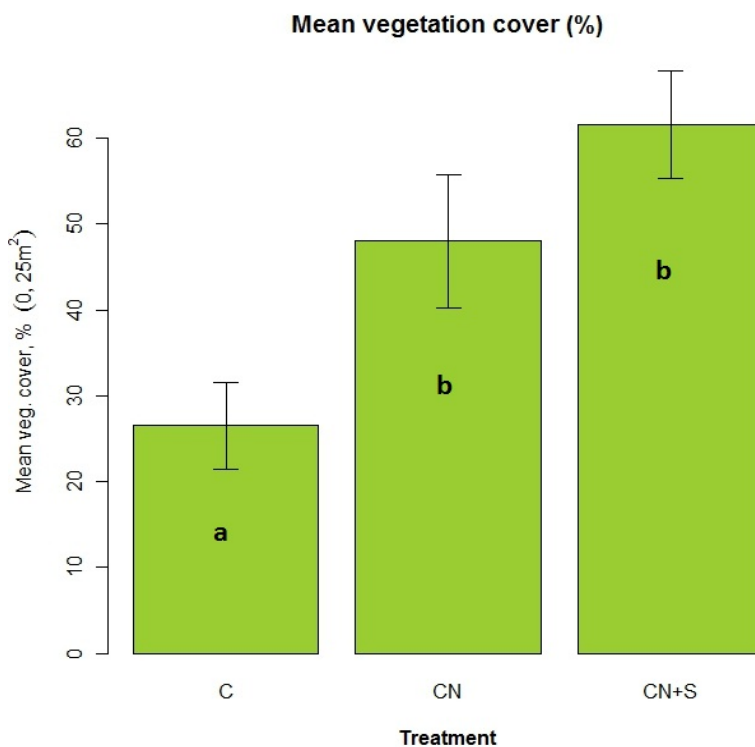


## RESULTS

We found no significant difference in overall vegetation structure between the two roads in three of the data sets with repeated ANOVA (Established vegetation:  $p = 0.692$ , Seed bank:  $p = 0.166$ , Field seedlings:  $p = 0.37$ ), and they are therefore treated as two replicates in the further results. We found some quantitative difference in treatment effect between the two roads in the seed rain data, and therefore included area as a nested random factor when analyzing this data.

### VEGETATION COVER

The results from the percentage vegetation cover estimation indicate that both treatments CN and CN+S significantly increases vegetation cover compared to the control treatment C (Figure 2;  $p = 0.024$ ). As seen from Figure 2 there also seems to be an increase in mean vegetation cover with fertilizer + seeding (CN+S) compared to only fertilizer (CN), but this increase was not statistically significant.



**Figure 2:** Estimated mean vegetation cover in %, with standard error bars, for each of the three treatments control (C), Control + Nutrients (CN) and Control, Nutrient + Seeds (CN+S). Estimates based on percentage vegetation cover in 0.25m<sup>2</sup> square frame plots, n=10 per treatment. Dissimilar letter notations refer to statistically significant differences ( $p < 0.05$ ).

## TOTAL EFFECT OF TREATMENT

The analyses of the established vegetation, seeds and seedlings in the different life cycle stages show that the treatments affect plant frequency in established vegetation, with increasing frequency of plants with the addition of nutrients, but addition of both seeds and nutrients did not increase the frequency of plants significantly compared to only nutrients (Table 2; CN increased mean plant frequency of 6.13 per frame compared to C, ANOVA,  $p = 0.005$ ; CN+S increased mean plant frequency of 5.17 per frame compared to C, ANOVA,  $p = 0.021$ )

In the seed rain there was a quantitatively different treatment effect in the two study sites, with a higher numbers of graminoid seeds in the nutrient treatment in one of the roads. The difference between the control treatment (C) and the nutrient treatment was not as pronounced in the road with lowest seed numbers, leading to the fact that the only significant overall effect was that of seeding (CN+S) compared to that of nutrients (CN), where the mean was 69 less seeds per seed trap when adding both seeds and nutrients, compared to only adding nutrients (Table 2; LME,  $p = 0.045$ ).

The germination from the seed bank was the most variable among the datasets, with massive germination from certain samples, and low from most others. The main effect was found in the seed addition treatment (CN+S; Table 2), with significantly less seedlings germinating than in the control treatment (mean of 1.06 fewer seedlings per sample, GLM,  $p = 0.016$ ). This was also less seedlings than found when adding only nutrients (Table 2; mean of 0.96 fewer seedlings per sample, GLM  $p = 0.022$ ).

The prevalent difference found for field seedlings was the mean increase of 7.48 seedlings counted per frame between the seeding treatment (CN+S) and the control treatment (C; ANOVA,  $p \leq 0.001$ ; Table 2). There was also a significant difference between treatment C and CN (mean of 5.3 more seedlings per frame in C, ANOVA,  $p = 0.006$ ), and between treatment CN and CN+S (mean of 2.18 more seedlings per frame in CN, ANOVA,  $p = 0.013$ ).

**Table 2:** General effects of treatment on frequency of plants/seed-/seedling numbers. Sorted by data source and treatment. For each treatment mean frequency/number ( $\pm$  standard error), and the statistical significance between contrasts of treatments are given for each data source. All statistically significant results ( $p < 0.05$ ) are marked with asterisk(s):  $p \leq 0.001$  '\*\*\*',  $p \leq 0.01$  '\*\*',  $p \leq 0.05$  '\*',  $p \leq 0.1$  '.',  $p \leq 1$  ''.

Source	Treatment	Mean ( $\pm$ SE)	Contrasts	P - value	
Established vegetation (ANOVA)	C	9.9 ( $\pm$ 1.72)	C – CN	0.005	**
	CN	16.03 ( $\pm$ 1.98)	C – CN+S	0.021	*
	CN+S	15.07 ( $\pm$ 1.25)	CN – CN+S	0.866	
Seed rain (LME)	C	22.05 ( $\pm$ 6.38)	C – CN	0.812	
	CN	93.95 ( $\pm$ 27.68)	C – CN+S	0.179	
	CN+S	24.87 ( $\pm$ 5.96)	CN – CN+S	0.045	*
Seedling in seed bank (GLM)	C	1.48 ( $\pm$ 0.59)	C – CN	0.890	
	CN	1.38 ( $\pm$ 0.80)	C – CN+S	0.016	*
	CN+S	0.42 ( $\pm$ 0.17)	CN – CN+S	0.022	*
Seedlings in field (ANOVA)	C	15.57 ( $\pm$ 1.76)	C – CN	0.006	**
	CN	10.27 ( $\pm$ 1.16)	C – CN+S	0.000	***
	CN+S	8.09 ( $\pm$ 1.26)	CN – CN+S	0.013	*

## TREATMENT EFFECTS ON FUNCTIONAL TYPES

The distribution and abundance effect of treatment on the functional plant types vary notably between the different stages (Figure 3).

### ESTABLISHED VEGETATION

The lowest frequency of dwarf shrubs is found in the control treatment (mean of 8.9 lower compared to CN+S, ANOVA,  $p = 0.008$ ). The fertilizer treatment CN yields the highest frequency of dwarf shrubs and graminoids, while the fertilizer and seeding treatment CN+S yields the highest frequency of forbs. In the established vegetation graminoid species had the highest frequency records through all treatments, still no differences between other growth forms came out significantly different between treatments.

### *SEED RAIN*

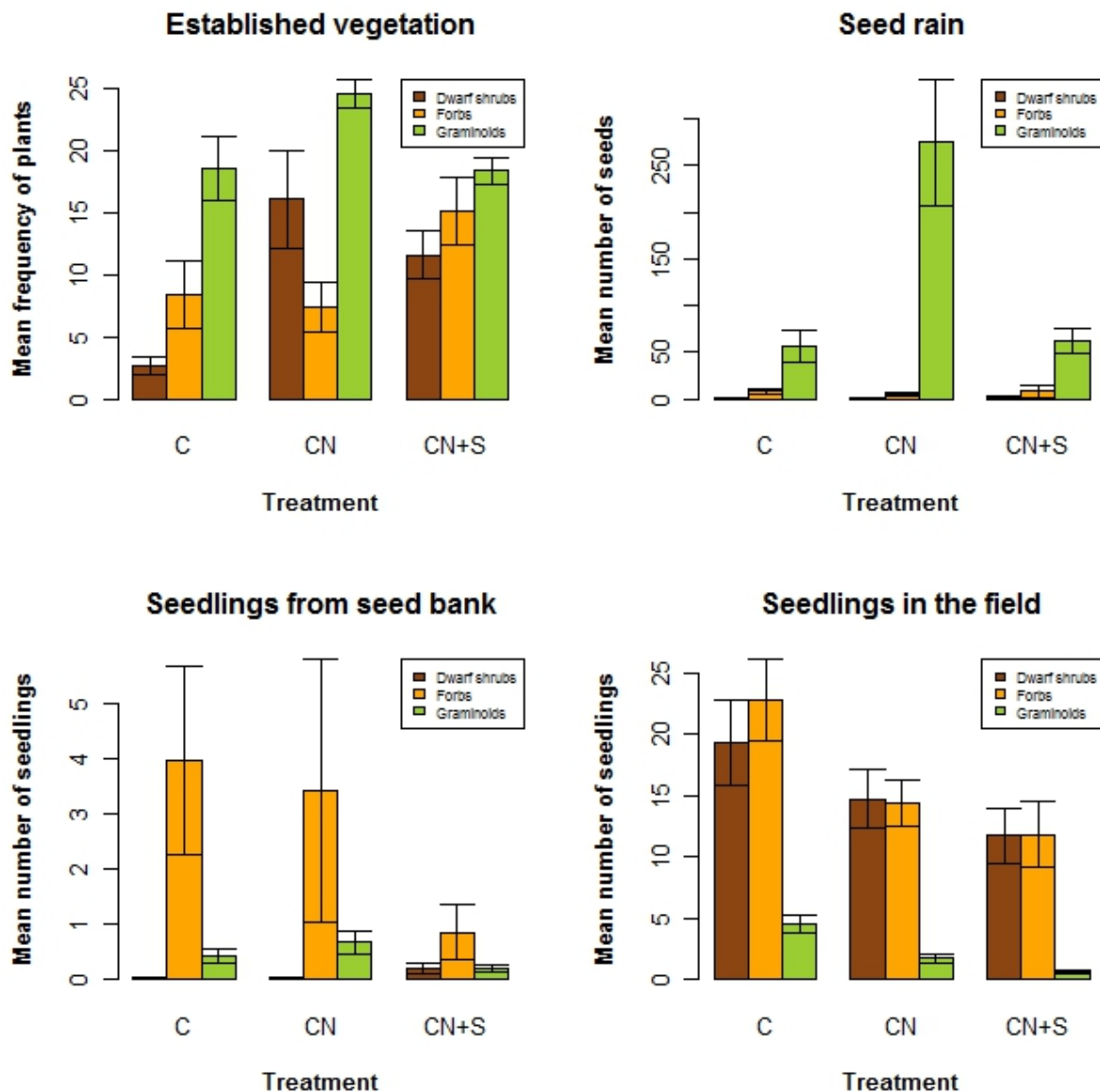
The seed rain analyses shows a highly significant increase in graminoid seeds in treatment CN compared to both treatment C and CN+S (Figure 3; a mean increase of approximately 216 more graminoid seeds per seed trap compared to the two others, LME,  $p = 0,009$ ). All other seed types are approximately equally distributed among the three treatments.

### *SEED BANK*

The number of seedlings germinating from the seed bank analyses was lower than the quantities found in other life cycle stages. As shown in Figure 3 there is also a quite substantial standard error of the mean, due to seed capsules creating extreme densities of seedlings in certain containers. There was overall very few dwarf shrubs germinating in all treatments, with a significant increase from a mean of 0 germinating dwarf shrubs per sample in C and CN to a mean of 0.20 in CN+S (GLM,  $p = 0.049$ ). Still, CN+S had significantly less forbs germinating than the two other treatments (approximately 2.65 fewer seedlings per sample, GLM,  $p = 0.001$ ). There was no significant difference between the mean number of either forbs or graminoids germinating from treatment C compared to CN, but CN had the highest number of graminoids germinating from the seed bank (mean of 0.475 more seedling per sample than CN+S, GLM,  $p = 0.004$ ). Treatment CN+S had the lowest number of graminoids, which was also significantly lower than in treatment C (mean reduction of 0.225 seedlings per sample, GLM,  $p = 0.013$ ).

### *FIELD SEEDLINGS*

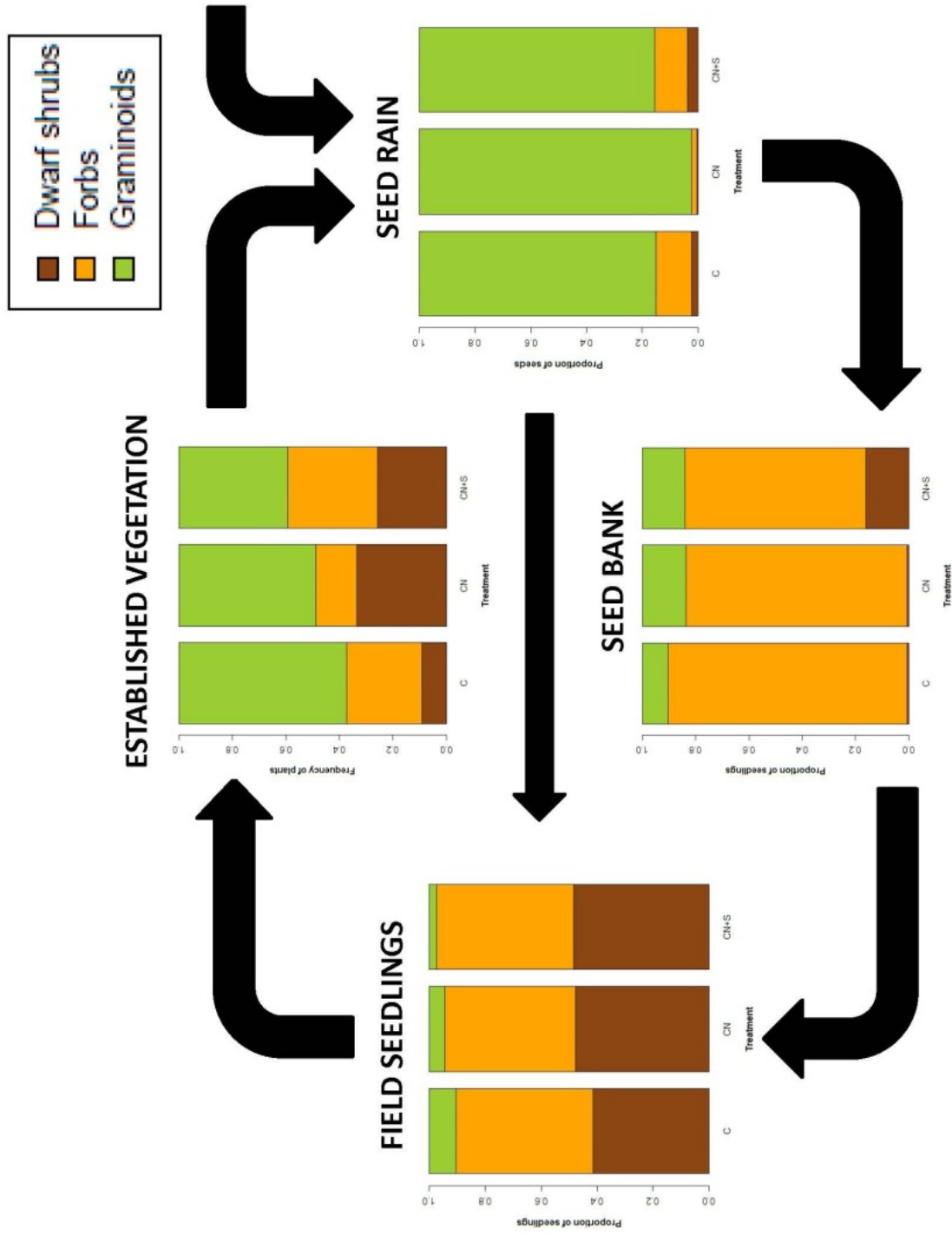
The naturally occurring seedlings in the field were not distributed equally to the established vegetation in the same areas. Most seedlings of all functional types were found in treatment C, still only the number of graminoids was significantly higher (mean increase of 2.77 seedlings per frame compared to CN, ANOVA,  $p = 0.066$ ; increase of 3.85 seedlings per frame compared to CN+S, ANOVA,  $p = 0.015$ ; Figure 3). Treatment CN+S had the lowest number of seedlings from all functional types.



**Figure 3:** The effect of treatment in four distinct phases of the regeneration pathway (Established vegetation, Seed rain, Seed bank and Field seedlings). Mean values  $\pm$  SE (per 0,25m<sup>2</sup> in established vegetation and field seedlings, per 0,1m<sup>2</sup> in seed traps and per 0.038 m<sup>2</sup> in seed bank). Treatments C, CN and CN+S refer to treatments as described in methods. All species are divided into three groups; Dwarf shrubs, forbs and graminoids. Overall effects of treatment with statistics for each stage in the regeneration pathway shown in Table 2, and for each functional group in appendix Table A3.

#### PROPORTIONAL CHANGES THROUGH THE REGENERATION PATHWAY

We compared the proportion of dwarf shrubs and forbs (dicot) and graminoids (monocot) within each treatment and life cycle stage, which revealed a great turnover in composition of functional types as we move from seed rain to established vegetation (Figure 4). While the seed rain is dominated by monocotyledon species (C=85 %, CN=98 %, CN+S= 84 %), dicotyledonous seeds dominate both the seed bank and the field seedlings.



**Figure 4:** All dwarf shrub, forb and graminoid units in the four different life cycle stages as a proportion of total number of units within each treatment. Accurate proportions in appendix Table A1, Table A2. There is a turnover from graminoid dominance in the seed rain, to forb dominance in the seed bank, and an approximately equal ratio of forbs and dwarf shrubs among the field seedlings, where the graminoids are least represented of all stages. The established vegetation has a higher proportion of graminoids compared to the field seedlings, but a lower proportion of dwarf shrubs.

The proportion of dwarf shrub seedlings are much higher among the seedlings germinating in the field than in the seed bank (C=42 %, CN=48 %, CN+S=49 %; compared to C=0.6 %, CN=0.6 %, CN+S=16%), and also compared to dwarf shrubs in the established vegetation (C=10 %, CN=34 %, CN+S=26 %). The seed bank is mainly dominated by forbs (C=90 %, CN=83 %, CN+S=68 %), and the established vegetation shows the most equal distribution among the functional types, though with a slight dominance of graminoids, especially in treatment C (63% compared to CN = 51%, CN+S = 41%).

## SPECIES EFFECTS

### DWARF SHRUBS

The late succession dwarf shrubs *Betula nana* and *Empetrum nigrum* did not seem especially affected by the different treatments (Figure 5). Still, *B. nana* occurs in a lower proportion in treatment CN in the established vegetation compared to C and CN+S, and is also slightly lower as field seedling proportions in treatment CN+S compared to C and CN. *E. nigrum* show no clear trend towards treatment response, with an exception of the increase in seedlings germinating from the seed bank in treatment CN+S (14% against 0.6% in C and CN), though this might partly be an artifact of a low total number of seedlings germinating from the seed bank. Both species show their highest abundances in the field seedling phase, where they actually make up a larger proportion of the total than they do in the established vegetation.

### FORBS

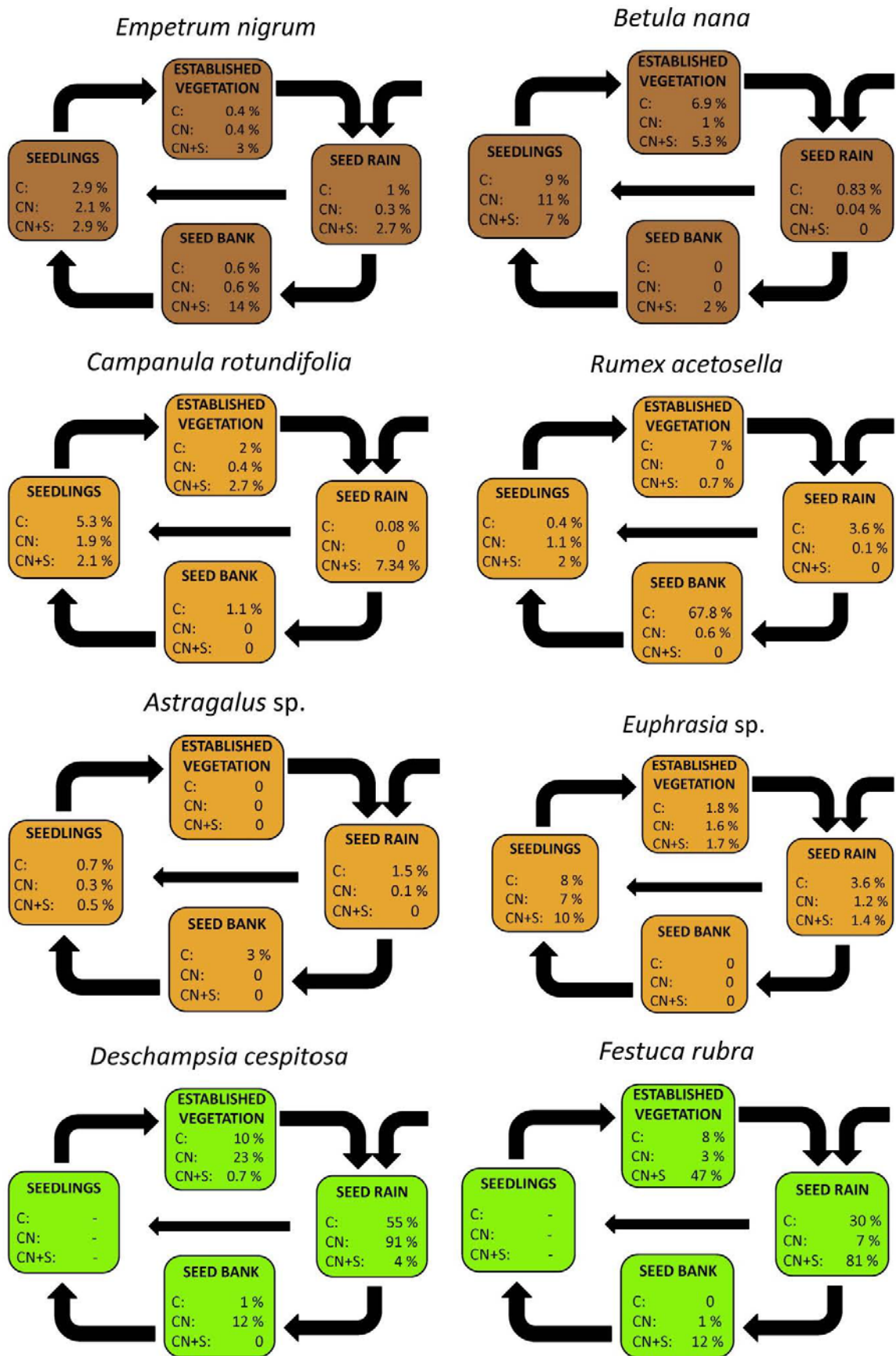
The forbs *Campanula rotundifolia* and *Rumex acetosella* appeared in all phases of the regeneration pathway, though in different abundances (Figure 5). *C. rotundifolia* was most common in the field seedling phase, where it had the largest proportion in treatment C compared to CN and CN+S, and it only germinated in treatment C in the seed bank. Through all phases, *C. rotundifolia* was rarest in treatment CN. *Rumex acetosella* appeared sporadically within each life cycle phase, with an all-time high constituting 67,8 % of all germinating seedlings from the seed bank in treatment C, while it was most commonly found in the field seedling phase in treatment CN. *Euphrasia* sp. appeared in all phases of the regeneration pathway except the seed bank, with no dramatic effect of treatment. It seems to be most common in the seedling phase, where it constituted 7-10% of the total in all treatment patches. *Astragalus* sp. was not recorded at all in the established vegetation. The seeds appeared in the seed rain in both treatment C and CN, and it also accounted for 3% of all germinating individuals in treatment C in the seed bank.

## GRAMINOIDS

Two species of graminoids dominated the study area; the seeded commercial *Festuca rubra*, and *Deschampsia cespitosa*. We believe that both species might have been found in all phases of the life cycle, but it was not possible to separate these species at the seedling level in the field. We might therefore confer with the overall proportion results for a merged monocot proportion at this stage (C= 10%, CN= 6 % CN+S= 3%; Figure 5). *F. rubra* seemed to dominate (47%) of the established vegetation in treatment CN+S during the survey in 2009, 7 years after seeding (Figure 5). *F. rubra* also dominated the seed rain the same area (account for 81% of all seeds). *F. rubra* in the seed rain C accounted for 30% of all seeds, which is higher than its proportion in the established vegetation. In the seed bank *F. rubra* seedlings mainly appeared in samples from treatment CN+S.

In the established vegetation *Deschampsia cespitosa* is most abundant in treatment CN (23%) followed by treatment C (10%), but is barely present in treatment CN+S (0,7 %). The same pattern is found in the seed rain, where *D. cespitosa* accounts for 91% of the seed rain in treatment CN, 55% in treatment C and only 4% in treatment CN+S. It also mainly germinated from seed bank samples from treatment CN (12%), with only one individual germinating from treatment C, and none from CN+S.





**Figure 5:** Proportion of eight selected species with different life histories as proportions of total number of units within each stage/treatment. Dwarf Shrubs: *Betula nana* and *Empetrum nigrum*. Forbs: *Rumex acetosella*, *Campanula rotundifolia*, *Astragalus sp.*, *Euphrasia sp.*, Graminoids: *Deschampsia cespitosa* and *Festuca rubra*.

## DISCUSSION

The nutrient treatment (CN) gave a dominance of *Deschampsia cespitosa*, a graminoid effective in nutrient utilization, which produced massive amounts of seeds and excluded the seeded *Festuca rubra* from these sites. The vegetation cover increased with nutrient addition both with and without additional seeding, resulting in less seedlings germinating in these areas. Still, there might be a higher rate of seedling survival in the nutrient treatments judging from the composition of the established vegetation. This indicates that suitable microsites for germination is more numerous in the less vegetated control sites, but that facilitation from neighboring vegetation perhaps occurs in later stages of the seedling establishment phase.

### TREATMENT EFFECTS ON VEGETATION COVER

#### SEED PRODUCTION AND ENTRAPMENT

It is assumed that arctic and alpine areas have slow growth and low nutrient turnover (Bowman et al. 1993), and graminoid species seems most able to take advantage of increased nutrient levels (Heer et al. 2002, Soudzilovskaia et al. 2005). The control treatment had significantly less vegetation cover compared to the two other treatments (Figure 2), and reduced seed production and entrapment should therefore be expected. We did observe less seed entrapment in controls compared to the nutrient treatment (CN), but the difference was not significant when comparing controls to the seeded sites (CN+S), which had the highest vegetation cover (Figure 2). This supports the idea that it is not the vegetation cover *per se* that controls seed entrapment, but rather an effect of species composition influencing seed output and vegetation structure.

The seed rain was dominated by graminoid species, which is common for both seed rain and standing vegetation in an early successional stage (Chambers 1993). One species, *Deschampsia cespitosa*, accounts for 91 % of the seed rain in area CN, while only representing 23% of the established vegetation (Figure 3), and there is reason to believe that the trapped seeds are produced by the same individuals that dominate the area, as most seeds are distributed close to their origin (Chambers et al. 1994). *D. cespitosa* has a “rapid potential growth strategy”, meaning that it can take advantage of increased resource availability in disturbed environments (Suding et al. 2004). The seeds of *D. cespitosa* is shown to have good germination capacity (Bu et al. 2006), and with the large seed production it was surprising to find that only 3-10 % of all seedlings recorded in the field were monocots (Figure 4). The seeds of *D. cespitosa* have awn appendages for effective

dispersal (Graae 2002), but these have been shown to limit seed burial, and thus seedling recruitment (Peart 1984). Graminoids represent a large proportion of the established vegetation in all sites, and while they usually are assumed to rely on vegetative reproduction in the alpine (Tschurr 1992, Welling et al. 2005), combining this with a capacity of massive seed production might provide competitive advantage compared to other functional groups.

#### GERMINATION AND ESTABLISHMENT

In our control treatment plots we found significantly more seedlings than the two other treatments, with a higher number of all three plant groups (Figure 3). Even though facilitation is traditionally seen as more important than competition in high elevation ecosystems, several studies are now showing results that seedlings compete with their neighbors also here (Forbis 2009, Klanderud 2010). With the control treatment having the lowest frequency of established vegetation, and the lowest input of seeds from the seed rain (Figure 3), the number of germinating seedlings in the field clearly indicates that availability of suitable microsites is a structuring force determining seedling establishment. In dense vegetation, moss or litter may limit soil contact, and thus prevent seedling emergence (Graae et al. 2011). Sufficient amounts of light are crucial for small seedlings, and we found graminoid seedlings in significantly lower numbers in the sites with elevated nutrient levels (CN, CN+S; Figure 3), which had a higher vegetation cover (Figure 2). This may reflect the low ability of certain graminoids to emerge as seedlings in vegetation with limited availability of light (Chambers et al. 1987, Grime et al. 1981).

Dwarf shrubs were found to have the highest germination in the field in the control plots, despite the significantly lower frequency of dwarf shrubs in the established vegetation (Figure 3). This indicates that sufficient microsites, with amongst other suitable light conditions due to the lower vegetation cover, are important for germination in this group. Similar results are shown also in other studies, with increased germination in gaps (Gough 2006, Graae et al. 2011, Klanderud 2010). Although the number of germinating seedlings increased, there has been reported high seedling mortality in dwarf shrubs such as *Betula nana* and *Salix sp* (Eckstein et al. 2011, Graae et al. 2011). Suitable sites for germination is not always suitable for seedling establishment and growth (Schupp 1995), which might lead to high seedling mortality in less sheltered microhabitats, and there is some evidence of facilitative effect of neighbors on *Betula* survival (Eckstein et al. 2011, Gough 2006). Succession in the alpine is considered a very slow process, and a timescale of roughly 50 years is common until certain stability in species composition can be perceived (Erschbamer et al. 2008), which means that the recorded species frequencies of the seven year old vegetation still is expected to go through several changes. Alpine ecosystems are also known to have less obvious successional stages than most other terrestrial ecosystems (Ebersole 2002, Macmahon 1980), which makes it hard to predict the future successional path of the

study sites. That our results show a higher proportion of seedlings than established dwarf shrubs, as well as higher seedling numbers in the control treatment compared to the fertilized treatments (CN, CN+S), might indicate successional change rather than high seedling mortality, which only future vegetation monitoring will reveal.

The response in seed and seedling numbers to the different treatments appears to depend upon specific traits of the species in question (Figure 5). Some species were dominating the seed bank in the control treatment (e.g. *Rumex acetosella*, *Sagina* sp.), but were hardly found as field seedlings. This indicates germination failure and/or seedling mortality, and facilitation from neighboring plants can enhance survival, which might explain the slightly higher field germination rate in the seeded (CN+S) sites. Seedling mortality in alpine and arctic habitats is concentrated during growing season rather than occurring in winter, with drought during summer as the key limiting factor for survival (Forbis 2003, Urbanska et al. 1986), and neighboring plants have been shown to relieve drought stress (Biaou et al. 2011). The capacity to take advantage of facilitation by neighboring plants has been described as a function of seed size, with larger seeds having increased germination ability in dense vegetation (Leishman et al. 1994), which could explain why dwarf shrubs such as *Empetrum nigrum* and *Betula nana* seems robust against graminoid competition (Figure 5).

The significant decrease in established dwarf shrubs in control areas compared to the others, points towards favorable facilitation effects of neighboring vegetation in this group. Small seeded species such as *Rumex acetosella* and *Campanula rotundifolia* (with the exception of a single loaded seed capsule in the seed rain of CN+S), seems to slightly prefer the untreated control sites (C, Figure 5). Litter and graminoid biomass accumulation has also been shown to suppress the species richness of forbs (Deak et al. 2011), which might explain the lower levels of forbs in the established vegetation in the nutrient treatment (CN) compared to the nutrient + seeded treatment (CN+S). *D. cespitosa*, with its rapid growth and tall stature (Alonso et al. 1998) should be expected to produce larger amounts of litter compared to *F. rubra*, but we found no indication of less seedlings in the nutrient treatment (CN) compared to the nutrient + fertilizer treatment (CN+S, Table 2, Figure 3).

#### EFFECTS APPEARING IN CERTAIN GROUPS, SPECIES OR LIFE HISTORY STAGES

The lower alpine zone of Norwegian mountains are typically dominated by the dwarf shrubs *Salix* sp. in moist habitats and *Betula nana* in xeric habitats (Ryvarden et al. 1995). The different growth forms considered in this study; dwarf shrubs, forbs and graminoids in represent different adaptations to cope with the alpine environmental conditions, differing in amongst other life span, seed size and numbers, flowering phenology and preferred

reproductive means (Crawley 1997), and we therefore expected differential response to the restoration treatments among these functional types.

Seven years after seeding, *F. rubra* still dominated the seeded site (CN+S), but the seeding did not increase the total proportion of graminoids in any stages of the life cycle, relative to the effect of nutrients alone (Figure 4). *F. rubra* seems less able to utilize the elevated nutrient levels compared to *D. cespitosa*, with lower total numbers of seeds recorded in the seed traps (Figure 5). Despite this, *D. cespitosa* is not capable of outcompeting *F. rubra* in the seeded sites. *D. cespitosa* is shown to be competitively displaced if water levels are lowered to the point where it can no longer grow or reproduce (Theodose et al. 1997), despite it being the most efficient nutrient utilizer, and this might be what we are observing here. Both species still coexist in the established vegetation in the control sites, indicating that vegetation cover here is too sparse for severe competitive interactions. This also indicates that the non-native *F. rubra* is able to spread outside the seeded areas, and it is discouraged to seed non-native species for recovery in such cases (Scherrer et al. 2006). While the *D. cespitosa* dominated areas (CN) in our study seem slightly more hospitable to seedlings in the field and seed bank compared to the *F. rubra* sites (CN+S; Figure 3), facilitating for *D. cespitosa* dominance might have severe consequences for future succession in the restored areas. Studies have shown this species to be an aggressive competitor due to its effective resource utilization (Kryszak et al. 2009, Theodose et al. 1997), and shading of other species has been discovered (Alonso et al. 1998). Biodiversity appears lower in *D. cespitosa* dominated grasslands compared to those of other species, and the fact that this graminoid has a low palatability to common grazers such as sheep increases the competitive ability further, as well as accumulating litter (Krahulec et al. 2001). *F. rubra* has also been shown to prevent seedling establishment, possibly due to a dense and shallow root system lowering soil moisture (Densmore 1992), but there are some indications that native *Festuca* seeds are less competitive (Hansen 2011).

The control areas have the highest proportion of graminoids (Figure 4), which is due to the low numbers of dwarf shrubs found here. Some of the dominant dwarf shrubs in the study area (*Empetrum nigrum*, *Betula nana*) are characterized as late successional, with *B. nana* being the slowest colonizer (Whittaker 1993). A trade-off between fecundity and life span (Forbis et al. 2004) might explain the sparse number of dwarf shrub seeds found in the seed rain (Figure 3). Low germinable seed bank (Figure 3), might be caused by the common dwarf shrub genus *Salix* sp., which are recorded to have transient seeds which persist in the soil for less than one year (Thompson 1997), and *Betula nana* and *Empetrum nigrum* are known to exhibit complicated germination requirements including cold stratification (Junttila 1970). The numerous dwarf shrub seedlings in the field however confirm that seeds are present, and *B. nana* has been shown to have high germination rates (Molau et al. 2000).

The forb species *Rumex acetosella* and *Sagina procumbens* dominating the seed bank seedlings (Figure 5), are both species ranked on the top 100 list of records in the seed bank of North west Europe (Thompson 1997). Certain alpine plants have adopted the strategy of short lived plants and long lived seeds which accumulate and persist in the seed bank (Cavieres 1999, Chambers 1993), and as neither of these species were common as established plants or seedlings in the field, this is probably what we are observing in our results. Both *R. acetosella* and *S. procumbens* have small seeds, which are often produced in higher numbers than larger seeds, but with the tradeoff that they are less capable of germinating and/or surviving in demanding environmental conditions as found in the field (Westoby et al. 1992). Such a strategy, known as *bet-hedging*, is not optimal in “average” years, but rather spreads the risk of short lives species going locally extinct during bad years in a fluctuating environment (Evans et al. 2007, Mathias et al. 2002).

Individuals from the genus *Euphrasia* sp. had the highest rate of seedlings in the field among the forbs (Figure 5), which might both be because it is less prone to competitive exclusion as a hemi-parasite (Svensson et al. 2004), but also reflect the trade-off between life span and fecundity, as *Euphrasia* sp. are annual forbs and therefore expected to have increased fertility (Forbis et al. 2004). The genus *Astragalus* sp. belongs to the nitrogen fixating legumes, which are described as particularly important during succession in nitrogen limited habitats (Li et al. 2010). Our results suggest that *Astragalus* sp. has a slight preference for the control sites (Figure 5), where this legume possibly finds more available microhabitats for germination, as it is not affected by nitrogen limitation. There were no recorded individuals of the genus *Astragalus* sp. in the established vegetation, which might either be due to the lower number of sampling units compared to the other stages, or that this genus is just now spreading from adjacent areas.

## CONCLUSION

Our study of the effect of restoration treatments on the regeneration pathway in alpine seed plants showed that nutrient and seeding treatments increased vegetation cover, which resulted in a negative effect on germination in the field in all functional groups. While germination benefited from microsite availability in sparse vegetation cover, we found indications of higher dwarf shrub seedling survival when growing in the nutrient and seeded treatment areas. The graminoid *Deschampsia cespitosa* dominated the nutrient treated areas, and was able to efficiently take advantage of the elevated nutrient levels through high seed production and probably clonal growth at the same time. The seeded sites were still dominated by the seeded non-native *Festuca rubra*, which also seemed able to spread as seeds in to the control areas, where the number of monocot seedlings were highest. The complex interactions between microsite availability and safe sites in successful seedling establishment complicate recommendations for future restoration attempts. *D. cespitosa* is shown to be an aggressive competitor reducing species richness, and sown non-native *F. rubra* in nearby areas have persisted and prevented rather than facilitated for the establishment of native species. Persisting meadows of graminoids will not blend in to the surrounding dwarf shrub heath, and is consequently not the desired target of the restoration attempts. There is indications that seeded native graminoids are less aggressive competitors than the above species, and might therefore be a suitable alternative to achieve facilitation without the loss of microsites for germination. Future monitoring of the established vegetation will reveal if the high recruitment of dwarf shrubs in the control plots speed up the establishment of the typical dwarf shrub cover similar to the surrounding vegetation and hereby indicate that unassisted recovery is the fastest way to restore alpine dwarf shrub heath.

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## APPENDIX

**Table A1:** All recorded species in the seed rain, seed bank and as field seedlings shown as a percentage (%) proportion of grand total within each data set and treatment, together with the growth form category of each species. Species names following Lid et al. (2005).

Species	Growth form	Seed rain			Seed bank			Field seedlings		
		C	CN	CN+S	C	CN	CN+S	C	CN	CN+S
<i>Arctostaphylos uva-ursii</i>	Dwarf shrub	0,08	-	0,13	-	-	-	-	-	-
<i>Betula nana</i>	Dwarf shrub	0,83	0,04	-	-	-	2,00	9,05	10,80	7,11
<i>Empetrum nigrum</i>	Dwarf shrub	0,98	0,30	2,74	0,56	0,61	14,00	2,94	2,11	2,88
<i>Juniperus sp</i>	Dwarf shrub	0,08	-	-	-	-	-	-	-	-
<i>Salix sp</i>	Dwarf shrub	0,08	0,04	0,77	-	-	-	29,55	34,82	38,52
<i>Vaccinium sp</i>	Dwarf shrub	0,15	-	-	-	-	-	-	-	-
<i>Achillea millefolium</i>	Forb	-	0,04	-	-	-	-	1,39	1,54	0,10
<i>Alchemilla sp</i>	Forb	-	0,02	-	-	-	-	-	-	-
<i>Antennaria Diocia</i>	Forb	0,53	0,14	0,51	0,56	-	-	7,60	6,49	17,51
<i>Arabadopsis sp</i>	Forb	-	-	-	0,56	0,61	-	-	-	-
<i>Astragalus alpinus</i>	Forb	-	-	-	2,26	-	-	-	-	-
<i>Astragalus norvegicus</i>	Forb	-	-	-	1,13	-	-	-	-	-
<i>Astragalus sp</i>	Forb	1,51	0,14	-	-	-	-	0,70	0,32	0,51
<i>Bistorta vivipara</i>	Forb	-	-	-	-	-	-	2,25	1,70	3,91
<i>Campanula rotundifolia</i>	Forb	0,08	-	7,34	1,13	-	-	5,30	1,95	2,06
<i>Cerastium alpinum</i>	Forb	-	0,09	-	-	-	-	0,32	0,73	-
<i>Erigeon acer</i>	Forb	-	-	-	-	-	-	0,80	2,11	-
<i>Euphrasia wettsteinii</i>	Forb	3,63	1,15	1,34	-	-	-	8,24	7,14	9,78
<i>Galium sp</i>	Forb	-	-	-	-	-	-	-	0,32	-
<i>Gentiana nivalis</i>	Forb	-	-	-	-	-	-	-	0,65	-
<i>Gentiana sp</i>	Forb	0,60	-	1,15	-	-	-	-	1,54	3,19
<i>Hieracium sp</i>	Forb	-	0,02	0,06	-	-	-	-	-	-
<i>Leontodon autumnalis</i>	Forb	1,66	0,09	0,26	-	-	-	-	-	-
<i>Pedicularis sp</i>	Forb	-	-	-	-	-	-	-	0,08	-
<i>Pinguicula vulgaris</i>	Forb	-	0,02	1,02	-	-	-	10,71	1,70	-
<i>Potentilla sp</i>	Forb	-	0,02	-	-	-	-	0,21	0,57	0,10
<i>Pusatilla Vernalis</i>	Forb	-	-	-	-	-	-	-	0,32	-
<i>Rumex acetosella</i>	Forb	3,55	0,11	-	67,80	0,61	-	0,37	1,06	1,96
<i>Sagina procumbens</i>	Forb	-	-	-	-	-	-	0,86	4,46	-
<i>Sagina saginoides</i>	Forb	-	-	-	14,12	81,21	66,00	-	-	-
<i>Sibbaldia procumbens</i>	Forb	-	-	-	-	-	-	0,05	-	-
<i>Solidago virgurea</i>	Forb	0,15	-	-	-	-	-	-	-	0,10
<i>Taraxacum sp</i>	Forb	-	0,02	-	-	-	-	-	-	-
<i>Thalictrum alpinum</i>	Forb	-	-	-	-	-	-	0,11	-	-
<i>Dicot (unknown)</i>	-	1,06	0,09	0,06	2,26	0,61	-	7,23	11,28	8,34
<i>Dicot (unknown)</i>	-	-	-	-	-	-	-	1,71	0,57	-
<i>Dicot (unknown)</i>	-	-	-	-	-	-	-	0,05	0,16	0,31
<i>Dicot (unknown)</i>	-	-	-	-	-	-	-	-	0,08	-
<i>Dicot (unknown)</i>	-	-	-	-	-	-	-	-	0,08	-
<i>Viscaria alpina</i>	Forb	-	-	-	-	-	2,00	0,91	1,79	0,93
<i>Viola sp</i>	Forb	-	-	0,13	-	-	-	-	-	-
<i>Agrostis cappilaris</i>	Graminoid	-	-	-	-	-	2,00	-	-	-
<i>Anthoxanthum sp.</i>	Graminoid	-	0,04	-	-	-	-	-	-	-
<i>Avenella flexuosa</i>	Graminoid	-	-	-	1,69	-	-	-	-	-

<i>Carex sp</i>	Graminoid	0,15	0,02	-	-	-	-	-	-	-
<i>Dechampsia cespitosa</i>	Graminoid	54,80	90,60	3,96	1,13	11,52	-	-	-	-
<i>Festuca ovina</i>	Graminoid	-	-	-	1,69	0,61	-	-	-	-
<i>Festuca rubra</i>	Graminoid	29,93	6,94	80,54	-	1,21	12,00	-	-	-
<i>Luzula sp</i>	Graminoid	0,15	0,11	-	2,82	1,21	2,00	0,43	0,49	-
<i>Monocot (unknown)</i>	Graminoid	-	-	-	2,26	1,82	-	8,73	5,11	2,68
<i>Poa alpine</i>	Graminoid	-	-	-	-	-	-	0,05	-	-
<i>Tofieldia pusilla</i>	Graminoid	-	-	-	-	-	-	0,43	-	-

**Table A2:** Cumulative frequency of each species in the established vegetation, on a scale from 0 to 160. Data included from all treatments, and the growth form of each species listed. Species names following Lid et al. (2005).

Species	Growth form	CN+S	C	CN
<i>Arctostaphylos uva-ursii</i>	Dwarf shrub	2	1	1
<i>Betula nana</i>	Dwarf shrub	16	31	48
<i>Betula pubescens</i>	Dwarf shrub	-	1	1
<i>Calluna vulgaris</i>	Dwarf shrub	-	-	1
<i>Empetrum nigrum</i>	Dwarf shrub	9	2	2
<i>Juniperus communis</i>	Dwarf shrub	1	-	-
<i>Salix glauca</i>	Dwarf shrub	2	21	37
<i>Salix lapponicum</i>	Dwarf shrub	-	2	8
<i>Salix phy</i>	Dwarf shrub	-	-	8
<i>Salix sp.</i>	Dwarf shrub	27	29	56
<i>Bistorta vivipara</i>	Forb	5	24	13
<i>Campanula rotundifolia</i>	Forb	8	9	2
<i>Cerastium alpinum</i>	Forb	-	7	2
<i>Diphysastrum alpinum</i>	Forb	1	-	-
<i>Equisetum arvense</i>	Forb		39	4
<i>Euphrasia wettisteinii</i>	Forb	5	8	7
<i>Gentiana nivalis</i>	Forb	10	-	1
<i>Leontodon autumnalis</i>	Forb	4	-	5
<i>Omalotheca supina</i>	Forb	3	5	3
<i>Oxytropis lapponicus</i>	Forb	1	8	3
<i>Potentilla crantzii</i>	Forb	-	1	10
<i>Potentilla sp.</i>	Forb	-	1	-
<i>Pulsatilla vernalis</i>	Forb	1	-	-
<i>Rumex acetosella</i>	Forb	2	30	-
<i>Sagina sp.</i>	Forb	-	-	1
<i>Solidago vir</i>	Forb	5	3	1
<i>Thalictrum alpinum</i>	Forb	2	-	-
<i>Trifolium repens</i>	Forb	-	-	2
<i>Viola sp.</i>	Forb	4		
<i>Viscaria alpina</i>	Forb	-	-	4
<i>Dechampsia cespitosa</i>	Graminoid	2	45	111
<i>Festuca ovina</i>	Graminoid	5	87	96
<i>Festuca rubra</i>	Graminoid	-	35	14
<i>Festuca rubra comm.</i>	Graminoid	141	-	-
<i>Festuca sp.</i>	Graminoid	-	13	-
<i>Graminoids</i>	Graminoid	-	6	1
<i>Luzula multiflora</i>	Graminoid	-	-	1
<i>Luzula sp.</i>	Graminoid	1	16	1
<i>Luzula spicata</i>	Graminoid	-	7	1

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<i>Poa alpina</i>	Graminoid	-	2	7
<i>Poa sp</i>	Graminoid	-	8	13
<i>Tofieldia Pusilla</i>	Graminoid	1	-	-

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**Table A3:** Statistical results from the comparison of treatment effects, Sorted by data source and treatment. For each treatment a mean frequency/number is listed with standard error, and the statistical significance between contrasts of treatments are given for each data source. All statistically significant results ( $p < 0.05$ ) are marked with asterisk(s):  $p \leq 0.001$  '\*\*\*',  $p \leq 0.01$  '\*\*',  $p \leq 0.05$  '\*',  $p \leq 0.1$  '.',  $p \leq 1$  ''.

	Type	Treat	Mean ( $\pm$ SE)	Contrasts	p-value	
Established vegetation	Dwarf shrub	C	2.7 ( $\pm$ 0.67)	C-CN	0.000	***
		CN	16.1 ( $\pm$ 4)	C-CN+S	0.008	**
		CN+S	11.6 ( $\pm$ 1.93)	CN-CN+S	0.905	
	Forb	C	8.4 ( $\pm$ 2.68)	C-CN	0.999	
		CN	7.4 ( $\pm$ 2.01)	C-CN+S	0.497	
		CN+S	15.2 ( $\pm$ 2.74)	CN-CN+S	0.308	
	Graminoids	C	18.6 ( $\pm$ 2.59)	C-CN	0.114	
		CN	24.6 ( $\pm$ 1.19)	C-CN+S	0.053	.
		CN+S	18.4 ( $\pm$ 1.12)	CN-CN+S	0.621	
Seed rain	Dwarf shrub	C	1.45 ( $\pm$ 0.36)	C-CN	0.374	
		CN	1.05 ( $\pm$ 0.49)	C-CN+S	0.606	
		CN+S	2.71 ( $\pm$ 1.43)	CN-CN+S	0.999	
	Forb	C	8.45 ( $\pm$ 2.35)	C-CN	0.589	
		CN	5.45 ( $\pm$ 2.58)	C-CN+S	0.259	
		CN+S	8.86 ( $\pm$ 6.59)	CN-CN+S	0.999	
	Graminoids	C	56.25 ( $\pm$ 16.72)	C-CN	0.003	**
		CN	275.35 ( $\pm$ 67.3)	C-CN+S	0.653	
		CN+S	63.05 ( $\pm$ 13.21)	CN-CN+S	0.009	**
Seed bank Seedlings	Dwarf shrub	C	0.025 ( $\pm$ 0.025)	C-CN	1.000	
		CN	0.025 ( $\pm$ 0.025)	C-CN+S	0.049	*
		CN+S	0.20 ( $\pm$ 0.09)	CN-CN+S	0.049	*
	Forb	C	3.975 ( $\pm$ 1.71)	C-CN	0.916	
		CN	3.425 ( $\pm$ 2.38)	C-CN+S	0.001	***
		CN+S	0.85 ( $\pm$ 0.5)	CN-CN+S	0.001	***
	Graminoids	C	0.425 ( $\pm$ 0.12)	C-CN	0.749	
		CN	0.675 ( $\pm$ 0.2)	C-CN+S	0.013	*
		CN+S	0.20 ( $\pm$ 0.07)	CN-CN+S	0.004	***
Field seedlings	Dwarf shrub	C	19.4 ( $\pm$ 3.48)	C-CN	0.482	
		CN	14.7 ( $\pm$ 2.4)	C-CN+S	0.125	
		CN+S	11.78 ( $\pm$ 2.26)	CN-CN+S	0.406	
	Forb	C	22.8 ( $\pm$ 3.31)	C-CN	0.654	
		CN	14.38 ( $\pm$ 1.91)	C-CN+S	0.119	
		CN+S	11.85 ( $\pm$ 2.68)	CN-CN+S	0.267	
	Graminoids	C	4.5 ( $\pm$ 0.71)	C-CN	0.066	.
		CN	1.73 ( $\pm$ 0.34)	C-CN+S	0.015	*
		CN+S	0.65 ( $\pm$ 0.11)	CN-CN+S	0.553	



