HØGSKOLEN i INNLANDET

Faculty of Applied Ecology and Agricultural Sciences

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Master Thesis

Recovery from experimental disturbance in alpine vegetation communities in central Norway

Master in Applied Ecology

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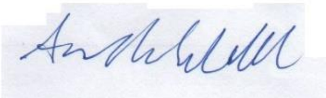

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Abstract

Human activity has increased in alpine environments during the last decades and is expected to continue to increase. Alpine habitats are highly sensitive to anthropogenic disturbance, such as trampling or motorized transportation, which often cause severe damage. Dispersal and growth rates are low due to short growing seasons, making recovery from severe disturbance a slow process. Therefore, increased knowledge about recovery from severe disturbance is needed to be able to reduce deleterious impacts from interventions in alpine habitats. In the present study, vascular plant recovery from nine-year-old experimental severe disturbance (removal of aboveground biomass) in central Norway was investigated. Three alpine habitat types (leesides, ridges and late melting snow beds) in two different sites with contrasting climate (oceanic and continental) was included in the study. Three measures of recovery were used, species richness, ground cover and functional group abundance. I found that recovery differed between the habitats and sites, emphasising the importance of site specific knowledge when planning management actions. Species richness was similar between treatments but that the compositions differed. Recovery was highest in leesides and late melting snow beds continental site, but in the oceanic site the habitat with highest recovery ridges. The abundance of forbs and graminoids had similar abundance between treatments while woody species had lower abundance in disturbed plots. Based on these results, deleterious disturbance needs to be avoided in areas of low species richness due to low recovery rates.

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1. Introduction

Anthropogenic disturbance is a well-studied subject around the world and often has deleterious effects on plant communities in alpine ecosystems (e.g. Felix *et al.* 1992; Cole 1995; Pickering & Growcock 2009). Recreational tourism has increased in Scandinavian alpine regions over the last few decades (Gossling & Hultman 2006). Trampling and motorized transportation can cause severe damage that affect species composition in vegetation communities by direct damage to the plants and by altering the physical environment (Grabherr 1982; Kevan *et al.* 1995).

Alpine ecosystems have a complex topography with a wide array of habitats and micro-climates. The Scandes is Europe's most northern mountain range, with 44 habitat types listed in the EU habitats directive (Sundseth 2009). The climate is oceanic in the west and continental to the east (Moen, Lillethun & Odland 1999). Vegetation growth and dispersal rates are generally low and limited by harsh climatic conditions and short growing season in alpine regions (Billings & Bliss 1959; Molau 1996; Cooper *et al.* 2004; Ladinig & Wagner 2005). The response to anthropogenic disturbance differs between habitats, and the severity is determined by disturbance intensity in combination with the physical properties and species composition of the habitat (Grabherr 1982; Ebersole 2002; Pascal & Pickering 2006; Dickson *et al.* 2008; Evju, Hagen & Hofgaard 2012). Recovery, i.e. the process by which an ecosystem achieves relative biological and physical stability, from severe anthropogenic disturbance is a slow process in alpine ecosystems (Walker *et al.* 1987; Grabherr & Nagy 2009; Rydgren *et al.* 2011). Species richness is generally believed to both reduce the effect of disturbance due to a variety in levels of tolerance, i.e. the ability to survive and reproduce in a disturbed environment (Gabriel & Talbot 1984), and to increase the recovery rate (Walker, Kinzig & Langridge 1999; Elmqvist *et al.* 2003). However, severe disturbance that alters the physical environment can result in a change in inter- and intraspecific competition that potentially could lead to a permanent alteration of the species composition (Dickson *et al.* 2008).

Human activities are expected to further increase in the Scandes (Haukeland, Grue & Veisten 2010). Therefore, it is vital for the preservation of alpine habitats and biodiversity to acquire more knowledge about the response of and recovery from anthropogenic disturbance in alpine ecosystems. A large part of the Scandes lies in the low alpine zone which generally alternate between ridge, leeside and snow bed habitats. Leesides have steady water availability and snow melt occurs in early summer, the vegetation consists of dwarf shrubs, forbs and graminoids. Ridges are dry habitats with the earliest snow melt between the habitats in the study, the vegetation is dominated by lichens and dwarf shrubs but generally have a low number of vascular plant species. Late melting snow beds have high water availability and late snow melt and is generally dominated by bryophytes and some species of forbs and graminoids. The dwarf shrub *Salix herbacea* can be locally dominant, particularly at the oceanic site (Moen, Lillethun & Odland 1999).

In this study, I investigated the effects of severe disturbance in a nine-year-old disturbance experiment in the Norwegian low alpine zone (Evju, Hagen & Hofgaard 2012). I analysed the recovery of the vegetation communities in three different habitat types, leeside, ridge and late melting snow bed, in two sites with different climate, oceanic and continental climate. Three measurements of recovery were used, species richness, ground cover (percent ground cover of vascular plants) and functional group abundance. To investigate recovery of species richness, I analysed the effects of treatment (severely disturbed vs. no disturbance), habitat and site. For ground cover, I analysed the effect of treatment, habitat, site and the interaction effects of treatment*habitat and treatment*site. For functional group abundance, I analysed the effect of treatment, habitat, site and the interaction effects of treatment*habitat and treatment*site. I predict that (1) over sites, habitats with higher species richness will have higher recovery and (2) the continental site, Hjerkinn, have higher recovery due to more stable snow cover during winter and higher species richness (Holten 2003).

2. Methods and material

2.1 Study area

The experiment was established in the Dovrefjell-Sunndalsfjella national park region, a high mountain region in central Norway. Several peaks reach altitudes above 2000 m a.s.l, with Snøhetta at 2286 m a.s.l as the highest in the region, sheltering the eastern area from oceanic-climatic influence. Two sites, each 1 km^2, were selected in the low alpine zone to represent conditions of alpine-oceanic and alpine-continental climate. Both sites are summer grazing area for domestic sheep and wild rein deer. Dovrefjell-Sunndalsfjella national park region are popular tourist areas with many trails and cabins for public use (Stiftelsen iNasjonalparker 2013).

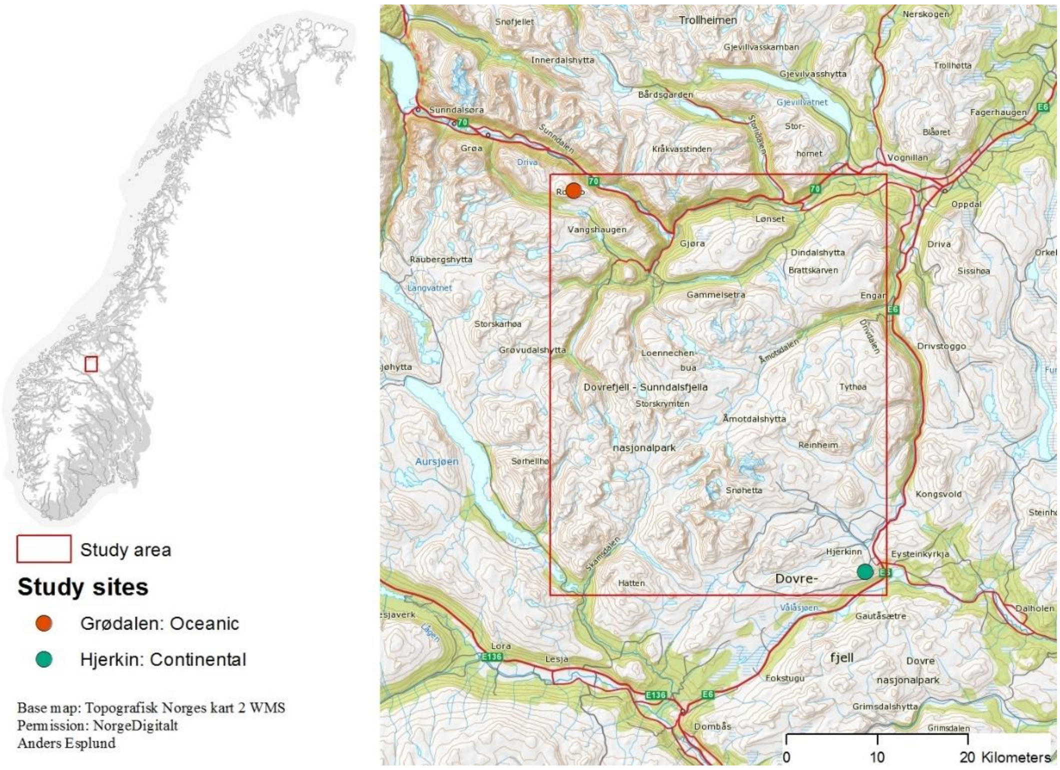

Figure 1. Overview of the study area

The site at Grødalen is located at around 1200 m a.s.l. in Sunndal municipality, Møre og Romsdal county (62°35'33''N, 8°53'44''E). The climate is slightly oceanic, O1, the bedrock is Precambrian gneiss, mainly tonalite or locally migmatite partly covered by a thin layer of till (Moen, Lillethun & Odland 1999; Norwegian Geological Survey 2016).

The site at Hjerkinn is located at around 1200 m a.s.l. in Dovre municipality, Oppland county (62°12'50''N, 9°30'47''E). The climate is slightly continental, C1, and the bedrock is metamorphosed phyllite and schist covered by a solid layer of till (Moen, Lillethun & Odland 1999; Norwegian Geological Survey 2016).

Hjerkinn is situated close to a former military training area that went out of commission in 1999 (Norwegian Ministry of Defence 1999). The area will be restored to its natural state and after completion it will be included in Dovrefjell-Sundalsfjella national park (Fylkesmannen i Oppland 2003). The area is now the largest nature restoration project in Norwegian history (Forsvarsbygg 2011). Hjerkinn is an important area for conservation of biodiversity. There is high species richness, with several red listed species of plants and it is an important breeding area for many bird species as well as part of the home range of the introduced musk ox population (Strand *et al.* 2013; Reitan *et al.* 2014).

2.2 Experimental setup

Three transects were subjectively selected in each study site (Grødalen and Hjerkinn) in 2007. Each transect contained three habitat types: leeside, ridge and late-melting snow bed. The size of each selected habitat was set to cover 20 x 20 m except for the snow bed habitats that were set to 10 x 40 m due to the shape of the habitat. All habitats had 12 permanent plots of 0.5 x 0.5 m (marked in each corner with metal nails) randomly located and each plot were randomly assigned to one of three disturbance types. In this study the two treatments used are: A; control (no disturbance) and C; severe disturbance (complete uprooting of vegetation, simulating severe trampling or motorized transportation). For full details of the experimental set up, see Evju *et.al* (2012).

Plots were located by pinpointing the metal nails in the plot corners with a metal detector. Three plots were excluded from the study, one plot in each site could not be found and one plot in Hjerkinn had been trampled.

The vegetation was analysed in each plot prior to being subjected to their respective disturbance treatments. In Hjerkinn, the plots were subjected to the treatments late in the growing season of 2007 but due to early snow fall in Grødalen treating the plots got delayed until early growing season of 2008. Vegetation analysis was done by registering the absence/presence of every vascular plant species in 16 subplots (12,5 x 12,5 cm) and percent vegetation- and soil cover was estimated. Unknown species were registered only as unknown forb or unknown graminoid, no unknown woody species was found. The plots were reanalysed in 2015 and 2016 in Hjerkinn and Grødalen respectively. For full details of the vegetation analysis, see Evju *et.al* (2012)

2.3 Statistical analysis

The data was processed in Microsoft Excel v. 16.0.7329.1045, all statistical analyses and illustrations were performed in R software v.1.2.136 (Morales 2012; R Core Team 2015).

To reveal the effects of severe disturbance on habitats (leeside, ridge and late-melting snow bed) three measurements of recovery were used: 1. Species richness, defined as. 2. Ground cover, defined as percent ground cover of vascular plants, and 3. Functional group abundance. To calculate functional group abundance, species were pooled into three functional groups, woody species, forbs and graminoids, unknown species was removed from the dataset. A measure of abundance was calculated by summarizing the subplot frequency for each species in every plot (appendix table 8) and divide the sum by 6,25 (one subplot = 6,25% of one plot) to get the number of subplot occurrences for every species. Functional group abundance is the sum of species abundance within each functional group.

To estimate the level of recovery, general linear models were fitted to the data and analysed with one- and two-way ANOVA, TukeyHSD was used to compare means in the models (Crawley 2002; R Core Team 2015). To investigate effects of disturbance on species richness, I analysed the effect of treatment, habitat and site on species richness. I also investigated the relationship between ground cover and species richness in disturbed plots with linear regression. To investigate effects of disturbance on ground cover, I analysed the effect of treatment, habitat, site and the interaction effect of treatment*habitat and treatment*site pooled over site. Furthermore, I analysed the effects of treatment, habitat and the interaction effects of treatment*habitat for each site separately. To compare the effect of treatment in each habitat between sites, I analysed the interaction of treatment*site in each habitat. To investigate effects of disturbance on functional group abundance, I analysed the effects of treatment, habitat, site and the interaction effects of treatment*habitat and treatment*site pooled over site. Furthermore, I analysed the effects of treatment, habitat and the interaction effects of treatment*habitat for each site separately. Finally, I compared the effects of treatment on the abundance of functional groups between sites by analysing the interaction effects of treatment*site on the abundance of all three functional groups in each habitat.

All models were checked for assumptions of normal distribution and homoscedasticity. All models were normally distributed and the variance of the residuals vs. fitted values were acceptable for most models. Several models, however, violated the assumptions of homoscedasticity and was either transformed with the natural logarithm (log) or square root (sqrt) of the response variable.

3. Results

3.1 Species richness

Seventy-five species of vascular plants were found in the study (appendix table 12), 41 in Grødalen and 66 in Hjerkinn and 32 species were found in both sites. Between sites, 9 species were found only in Grødalen and 34 was unique to Hjerkinn. Several species were only found in either control- or disturbed plots. In Grødalen, 34 species were found in control and 36 species in disturbed plots, the number of unique species in each treatment was 5 species in control- and 7 species in disturbed plots. In Hjerkinn, 50 species were found in control and 62 species in disturbed plots, the numbers of species unique to their treatment were 4 in control plots and 16 in disturbed. No significant difference in species richness was found between treatments. There is a significant difference in number of species between habitats and between the sites (fig. 2, table 1). As there was no effect of treatment, interactions were removed from the model. There was an overall positive linear relationship between species richness and ground cover in the disturbed plots (fig. 2) showing that average ground cover is higher in disturbed plots with higher species richness.

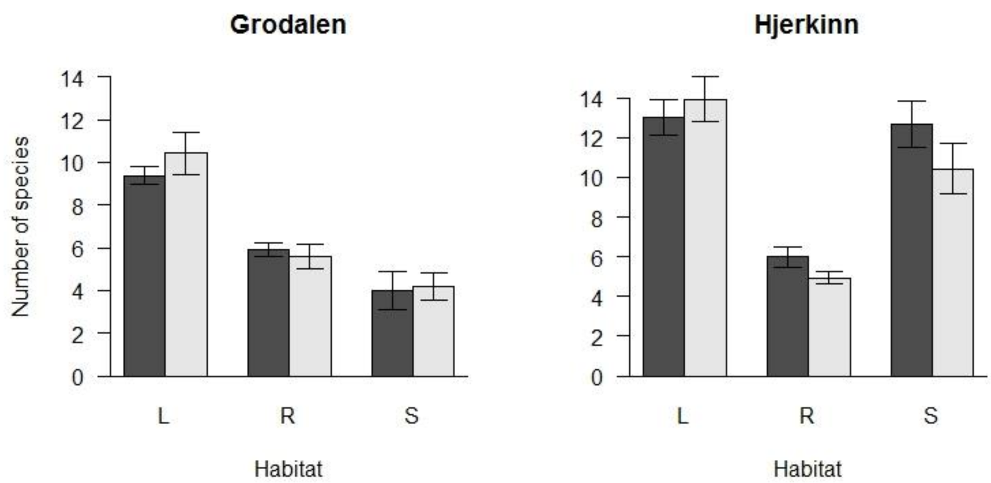

Figure 2. Mean number of species (± standard error) in control (grey) and disturbed (white) plots in leeside (L), ridges (R) and snow beds(S) of each site, Grødalen and Hjerkinn.

Table 1. Number of species as a function of treatment, habitat and site. $R^2 = 0.46$

Parameters	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	10.05	0.63	15.97	<0.001
Severe disturbance	-0.30	0.56	-0.53	0.595
Ridge vs. leeside	-6.06	0.68	-8.87	<0.001
Snow bed vs. leeside	-3.89	0.68	-5.72	<0.001
Hjerkinn vs. Grødalen	3.60	0.56	6.48	<0.001

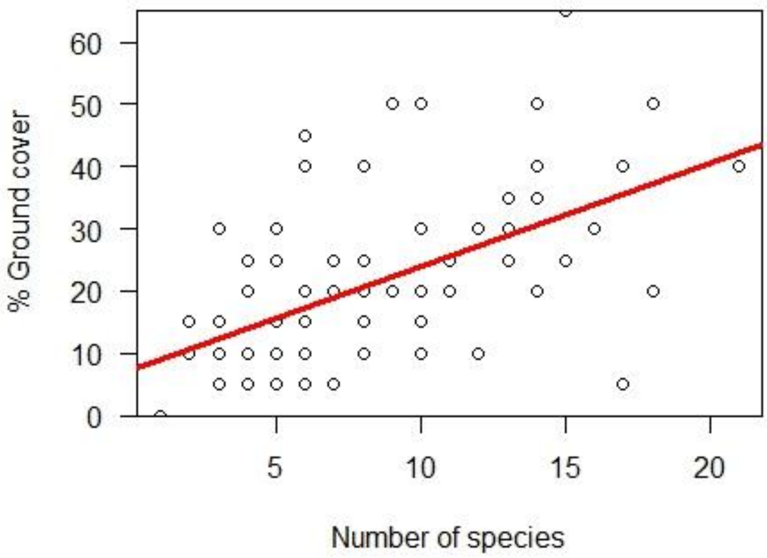

Figure 3. Positive linear relation between species richness and ground cover in disturbed plots

3.2 Ground cover

Ground cover was significantly lower in disturbed plots than in control plots (p = <0.001; fig. 4). There was a significant difference in ground cover between habitats (table 2). Leesides had higher average ground cover than both ridges and late melting snow beds when pooled over site and treatment. Ridges had lower average ground cover than late melting snow beds (p = <0.001). Ground cover differed significantly between the sites (p = 0.014) when pooled over treatment, and Hjerkinn had higher average ground cover than Grødalen. No significance was found in the treatment*habitat interaction when pooled over sites. But there was a significant treatment*site interaction (p = 0.018), as the effect of disturbance was larger in Grødalen than in Hjerkinn.

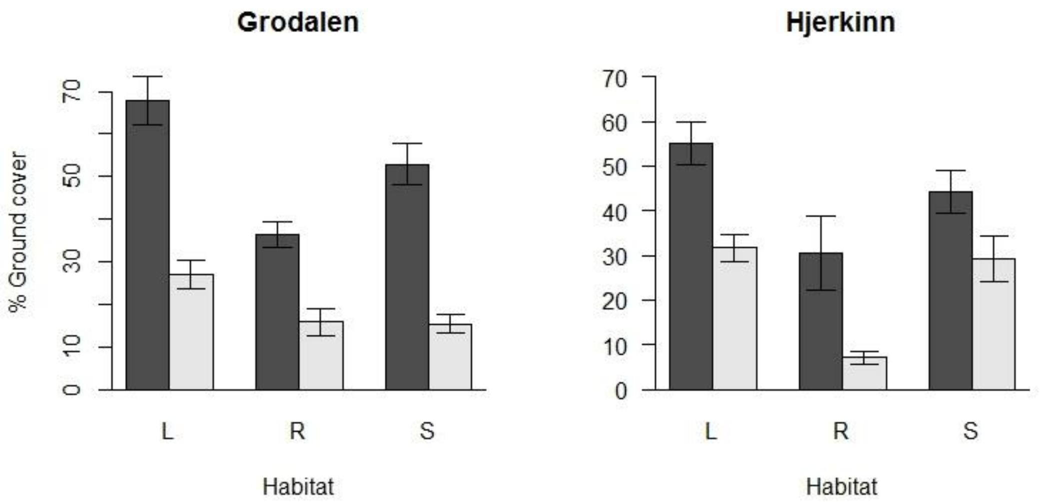

Figure 4. Mean ground cover (± standard error) in control (grey) and disturbed (white) plots in leeside (L), ridges (R) and snow beds(S) of each site, Grødalen and Hjerkinn.

Analysing the data for Grødalen revealed that the ground cover in disturbed plots was significantly lower than control plots. Between habitats, the average ground cover was significantly higher in leeside habitats than both ridge and late melting snow bed habitats. No significant difference was found in average ground cover between ridges and late melting snow beds (p = 0.089). There was a significant disturbance*habitat interaction between leeside and ridge habitats (p = 0.009), showing that ridges had higher recovery than leesides.

No significance was found for treatment*habitat between leeside and late melting snow bed habitats (appendix table 1).

In Hjerkinn, the ground cover was significantly lower in disturbed plots than in control plots. Leesides had significantly higher average ground cover than ridges. There was no difference between leesides and late melting snow beds. But ridges had significantly lower average ground cover than late melting snow beds (p = 0.001). No significant treatment*habitat interaction was found in Hjerkinn (appendix table 1).

Comparing the effect of disturbance in each habitat between sites revealed that there was a significant treatment*site interaction for leesides (p = 0.044, appendix table 2) and late melting snow beds (p = 0.013) but not for ridges (p = 0.792). The effect of disturbance was greater in Grødalen in both leesides and late melting snow beds.

*Table 2. Ground cover as a function of treatment, habitat, site and the interactions of treatment*habitat and treatment*site, $R^2 = 0.54$.*

Parameters	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	66.00	3.72	17.72	<0.001
Severe disturbance	-38.22	5.17	-7.40	<0.001
Ridge vs. leeside	-28.17	4.54	-6.21	<0.001
Snow bed vs. leeside	-12.91	4.49	-2.88	0.005
Hjerkinn vs. Grødalen	-9.09	3.66	-2.48	0.014
Disturbance x habitat (ridge)	10.26	6.31	1.63	0.107
Disturbance x habitat (snow bed)	5.83	6.28	0.93	0.355
Disturbance x Site	12.29	5.13	2.40	0.018

3.3 Functional group abundance

Average abundance of woody species was significantly lower in disturbed pots than in control plots when analysing the data pooled over sites (table 3). Between habitats, woody species had significantly higher average abundance in leesides than in both ridges and late melting snow beds (fig 5, table 3). Ridges had lower average abundance than late melting snow beds ($p = <0.001$). There was higher average abundance of woody species in Grødalen. No treatment*habitat or treatment*site interactions was found for woody species. For forb abundance there was no difference between disturbed plots and undisturbed plots. Between habitats, average abundance of forbs was higher in leesides than both ridges and late melting snow beds. Ridges had lower average abundance than late melting snow beds ($p = <0.001$). Hjerkinn had higher average abundance of forbs than Grødalen. No treatment*habitat or treatment*site interactions was found for forbs. For graminoids No difference in average abundance was found between treatments. Leesides had higher average graminoid abundance than both ridges and late melting snow beds. Ridges had lower abundance than late melting snow beds ($p = <0.001$). There was higher average abundance of graminoids in Hjerkinn. No treatment*habitat or treatment*site interaction was found.

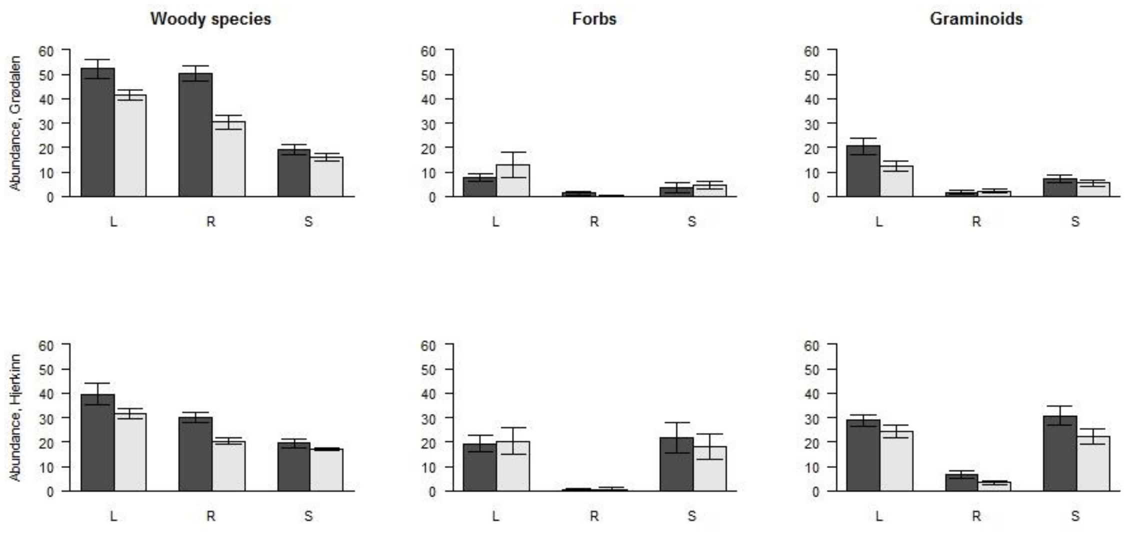

Figure 5.Mean functional group abundance (± standard error) in control (grey) and disturbed (white) plots in leeside (L), ridges (R) and snow beds(S) of each site, Grødalen and Hjerkinn.

Grødalen

Woody species had significantly lower abundance in disturbed plots than in control plots (fig. 5, appendix table 5). There was no significant difference in average abundance between leesides and ridges, but leesides had higher abundance than late melting snow beds. Ridges had higher abundance than late melting snow beds (p = <0.001). No treatment*habitat interaction was found for woody species. Forb abundance did not differ significantly between treatments. Leesides had significantly higher average abundance of forbs than both ridges and late melting snow beds, but there was no difference between ridges and late melting snow beds (p = 0.101). No treatment*habitat interaction was found (fig. 5, appendix table 8). Graminoids did not have a significant difference between treatment (fig. 5, appendix table 11). Between habitats, leesides had higher abundance than both ridges and late melting snow beds. Late melting snow beds had higher abundance of graminoids than ridges (p = 0.003, fig. 5). There was no significant treatment*habitat interaction.

Hjerkinn

Woody species abundance did not differ significantly between treatments (fig. 5, appendix table 5). Average abundance did not differ significantly between leesides and ridges, but both had higher than late melting snow beds. Ridges had higher abundance than late melting snow beds (p = 0.002). No significant treatment*habitat interaction was found for woody species. Forbs did not differ significantly between treatments (fig. 5, appendix table 8). Between habitats, leesides had higher abundance than ridges but not higher than late melting snow beds. Late melting snow beds had higher abundance of forbs than ridges (p = <0.001). No treatment*habitat interaction was found for forbs. Graminoids abundance did not differ significantly between treatments (fig. 5, appendix table 7). Between habitats, leesides had higher average abundance than ridges, but not higher than late melting snow beds. Ridges had lower abundance of graminoids than late melting snow beds (p = <0.001). No significant treatment*habitat interaction was found for graminoids.

Comparing the recovery of functional group abundance in each habitat between sites revealed that there was an interaction effect of treatment*site for woody species in ridges (p = 0.041, appendix table 4, 7 and 10), recovery was higher in Hjerkinn. No other interaction effect of treatment*site was found for any other habitat or functional group.

*Table 3. Abundance of functional groups as a function of treatment, habitat and site and interactions between treatment*habitat and treatment*site. Data pooled over site. For full table of the models see appendix table 3, 6 and 9.*

	P value		
Parameters	**Woody species**	**Forbs**	**Graminoids**
	$R^2 = 0.61$	*$R^2 = 0.41$*	*$R^2 = 0.60$*
Intercept	<0.001	<0.001	<0.001
Severe disturbance	<0.001	0.505	0.295
Ridge vs. leeside	0.047	<0.001	<0.001
Snow bed vs. leeside	<0.001	0.014	0.016
Hjerkinn vs. Grødalen	<0.001	0.002	<0.001
Disturbance x habitat (ridge)	0.136	0.841	0.405
Disturbance x habitat (snow bed)	0.083	0.305	0.831
Disturbance x site	0.160	0.917	0.289

4. Discussion

4.1 High species richness in early succession

Average species richness was similar in disturbed and control plots. There was, however, a difference in species composition, i.e. several species were found exclusively in disturbed or control plots. When comparing the sites, average species richness was greater in Hjerkinn which had higher species richness in both leesides and late melting snow beds while ridges had just about equal number of species in both sites. The continental climate in Hjerkinn is beneficial for species richness, as the more stable snow cover provide shelter from frost damage or winter desiccation (Holten 2003; Virtanen *et al.* 2003). Higher precipitation in the oceanic site is also likely to contribute to the large difference in species richness in late melting snow beds due to greater snow depth, making growing seasons in the habitat shorter in Grødalen (Billings & Bliss 1959; Galen & Stanton 1995). The results showed that species richness was fully recovered, but for species richness to have been fully recovered, the species composition should have been more similar between treatments. The species community is still in an early successional stage and species found only in control plots are likely to be climax species whereas species exclusive to the disturbed plots are pioneer species (Walker *et al.* 1987; Walker & del Moral 2003). A more thorough investigation of species composition should provide more detailed information about community recovery (Rydgren *et al.* 2011).

4.2 Vegetation recovery, faster in continental climate

Ground cover was lower in disturbed then it was in undisturbed plots. Average ground cover was higher in Grødalen but the effect of disturbance was also greater there, i.e. ground cover in disturbed plots were lower in Grødalen compared to Hjerkinn. As predicted, the highest recovery was found in Hjerkinn, more specifically, in leesides and late melting snow beds which also were the habitats with highest species richness, supporting the hypothesis of species richness (Elmqvist *et al.* 2003). Late melting snow beds have shorter growing season than the other habitats and was expected to have lower recovery than leesides. It seems, however, that high species richness and abundance of graminoids, likely due to stable water availability, increases recovery (Billings & Bliss 1959). The thin snow cover in the continental climate also allow for earlier snow melt, increasing the length of the growing season in snow beds compared to Grødalen.

In Grødalen, disturbed plots had lower ground cover in ridges than leesides, but recovery (i.e. percent ground cover in disturbed plots vs. control) was, contrary to my predictions, higher in ridges. Dry habitats with low species richness like ridges were expected to have lower recovery potential than habitats like leesides (Speed *et al.* 2010). The oceanic climate in Grødalen is likely to support growth throughout the growing season and thereby aiding recovery.

4.3 Functional group abundance is high, but mass is low

Of the three functional groups, only woody species in leesides and ridges had significantly lower abundance in disturbed plots compared to control plots. Vegetation removal may allow for rapid emergence of seedlings due to reduced competition, allowing for high abundance relatively soon after disturbance exposure (Klanderud 2010). Average abundance of woody species was higher in Grødalen but the average abundance of both forbs and graminoids were higher in Hjerkinn. There was little difference in recovery of functional group abundance between the sites, but recovery of woody species in ridges was higher in Hjerkinn. Growth of woody species, however, in both leesides and ridges seems to have been faster in Grødalen, i.e. there was higher abundance in the disturbed plots compared to Hjerkinn.

Forb and graminoid abundance was similar between treatments in all three habitats, but forb abundance in leesides was, though insignificantly, slightly higher in the disturbed plots than in the undisturbed plots. It is expected that forbs and graminoids recover faster than woody species (Speed *et al.* 2010), the latter generally having slower growth and dispersal rate (Lavorel *et al.* 1997). However, functional group abundance does not take individual number or plant size into account, individuals in disturbed plots were generally both lower in numbers and smaller in size than they were in undisturbed plots. So, there is likely a size- and or number bias in the small plot frequency method used, i.e. even though the frequency of forbs and graminoids did not differ between treatments, the total mass of all three functional groups was lower in disturbed plots than in undisturbed plots.

4.4 Study limitations

Ground cover was visually estimated by four different people, so the estimates could potentially be biased, but measures were taken to ensure equal estimates, and sub plots provided a good frame of reference for six percent of the plot. The three measures used here provide useful insight in the process of recovery from severe disturbance, but they do not reveal the full picture of recovery, particularly regarding the species composition. Methods like multidimensional scaling to investigate the variation of species composition between treatments, habitats and sites or principal response curves to reveal community response over time could have been a good compliment (Minchin 1987; Van den Brink & Braak 1999).

4.5 Management relevance

Alpine vegetation recovery is a slow process (Rydgren *et al.* 2011), and my results show that recovery differs between habitats and sites. This illustrates the importance of site specific knowledge in nature management. Disturbance should be avoided in ridges and leesides as these habitats generally have low tolerance (Evju, Hagen & Hofgaard 2012). Habitats with low species richness, i.e. leesides in Grødalen and late melting snow beds in Hjerkinn, also recover the slowest. Areas with high species richness is commonly prioritised in nature management, I show here that areas with lower diversity also needs be taken into consideration by natural resource managers when planning interventions in alpine ecosystems. As future use of alpine environments continues to increase, incorporating this knowledge about recovery from severe anthropological disturbance will be crucial to prevent deleterious impacts on ecosystems and to plan effective mitigation efforts.

4.6 Concluding remarks

Vegetation recovery is a complicated process with many biotic- and abiotic factors affecting every level of succession until the vegetation community reaches a stable state (Walker *et al.* 1987). The present results provide insight in early successional stages of vegetation recovery in Norwegian alpine environments. Species richness was similar in disturbed and undisturbed plots and species composition differed between treatments. Recovery of vegetation cover was higher in Hjerkinn, in habitats of high species richness. In Grødalen, ridges had highest recovery due to low vegetation cover in undisturbed plots, but leesides had the highest ground cover in undisturbed plots. Fast growing functional groups, forbs and graminoids, had higher abundance than slow growing woody species.

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Appendix

*Table 1. Ground cover as a function of treatment, habitat and the interaction of treatment*habitat. Data separated by site*

Grødalen, $R^2 = 0.67$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	67.91	3.96	17.17	<0.001
Severe disturbance	-40.83	5.48	-7.46	<0.001
Ridge vs. leeside	-31.66	5.48	-5.78	<0.001
Snow bed vs. leeside	-14.99	5.48	-2.74	0.008
Disturbance x habitat (ridge)	20.41	7.66	2.66	0.009
Disturbance x habitat (snow bed)	3.32	7.66	0.43	0.665
Hjerkinn, $R^2 = 0.41$				
Intercept	55.00	5.04	10.91	<0.001
Severe disturbance	-23.33	6.98	-3.34	0.001
Ridge vs. leeside	-24.55	7.13	-3.44	0.001
Snow bed vs. leeside	-10.83	6.98	-1.55	0.126
Disturbance x habitat (ridge)	-0.04	9.87	-0.00	0.997
Disturbance x habitat (snow bed)	8.33	9.76	0.85	0.397

*Table 2. Interactions of treatment*site in each habitat. Models for ridges and snow beds are square root transformed.*

Leeside, $R^2 = 0.57$	**estimate**	**standard error**	**t-value**	**p-value**

Intercept	67.91	4.31	15.78	<0.001
Disturbance x site	17.49	8.43	2.08	0.044
Ridge, $R^2 = 0.42$				
Intercept	5.95	0.43	13.80	<0.001
Disturbance x site	-0.23	0.87	-0.27	0.792
Snow bed, $R^2 = 0.47$				
Intercept	7.18	0.38	18.75	<0.001
Disturbance x site	1.99	0.77	2.60	0.013

*Table 3. Abundance of woody species as a function of treatment, habitat and site and interactions between treatment*habitat and treatment*site. Data pooled over site.*

Woody species, $R^2 = 0.61$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	51.27	2.25	22.79	<0.001
Severe disturbance	-11.56	3.12	-3.70	<0.001
Ridge vs. leeside	-5.49	2.74	-2.00	0.047
Snow bed vs. leeside	-26.62	2.71	-9.82	<0.001
Hjerkinn vs. Grødalen	-10.62	2.21	-4.80	<0.001
Disturbance x habitat (ridge)	-5.72	3.81	-1.50	0.136
Disturbance x habitat (snow bed)	6.62	3.79	1.75	0.083
Disturbance x site	4.37	3.10	1.41	0.160

*Table 4. Interactions of treatment*site on woody species abundance in each habitat*

Leeside, $R^2 = 0.28$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	52.27	3.28	15.93	<0.001
Disturbance x site	2.80	6.43	0.44	0.665
Ridge, $R^2 = 0.63$				
Intercept	50.42	2.41	20.94	<0.001
Disturbance x site	10.24	4.87	2.10	0.041
Snow bed, $R^2 = 0.00$				
Intercept	19.08	1.66	11.50	<0.001
Disturbance x site	0.67	3.32	0.20	0.842

*Table 5. Abundance of woody species as a function of treatment, habitat and the interaction between treatment*habitat. Data separated by site. Model for Hjerkinn is log transformed*

Grødalen, $R^2 = 0.70$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	52.27	2.79	18.71	<0.001
Severe disturbance	-10.77	3.87	-2.79	0.007
Ridge vs. leeside	-1.86	3.87	-0.48	0.630
Snow bed vs. leeside	-33.19	3.87	-8.58	<0.001
Disturbance x habitat (ridge)	-9.23	5.41	-1.71	0.093
Disturbance x habitat (snow bed)	7.69	5.41	1.42	0.160
Hjerkinn, $R^2 = 0.51$				

Intercept	3.63	0.08	45.78	<0.001
Severe disturbance	-0.18	0.11	-1.59	0.116
Ridge vs. leeside	-0.22	0.11	-1.98	0.052
Snow bed vs. leeside	-0.64	0.11	-5.82	<0.001
Disturbance x habitat (ridge)	-0.20	0.16	-1.30	0.197
Disturbance x habitat (snow bed)	0.07	0.15	0.47	0.638

*Table 6. Log transformed abundance of forbs as a function of treatment, habitat and site and interactions between treatment*habitat and treatment*site. Data pooled over site.*

Forbs, $R^2 = 0.41$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	1.95	0.27	7.32	<0.001
Severe disturbance	-0.25	0.37	-0.67	0.505
Ridge vs. leeside	-2.03	0.33	-6.23	<0.001
Snow bed vs. leeside	-0.80	0.32	-2.50	0.014
Hjerkinn vs. Grødalen	0.82	0.26	3.12	0.002
Disturbance x habitat (ridge)	0.09	0.45	0.20	0.841
Disturbance x habitat (snow bed)	0.46	0.45	1.03	0.305
Disturbance x site	-0.04	0.37	-0.10	0.917

*Table 7. Log transformed interactions of treatment*site on forb abundance in each habitat*

Leeside, $R^2 = 0.12$	**estimate**	**standard error**	**t-value**	**p-value**

Intercept	1.91	0.35	5.49	<0.001
Disturbance x site	0.15	0.68	0.22	0.829
Ridge, *R^2 = -0.01*				
Intercept	0.46	0.17	2.69	0.010
Disturbance x site	0.44	0.35	1.26	0.214
Snow bed, *R^2 = 0.24*				
Intercept	0.66	0.36	1.80	0.079
Disturbance x site	-0.66	0.73	-0.91	0.370

*Table 8. Log transformed abundance of forbs as a function of treatment, habitat and the interaction between treatment*habitat. Data separated by site.*

Grødalen, *R^2 = 0.22*	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	1.91	0.32	5.93	<0.001
Severe disturbance	-0.34	0.45	-0.76	0.448
Ridge vs. leeside	-1.44	0.45	-3.24	0.002
Snow bed vs. leeside	-1.25	0.45	-2.81	0.007
Disturbance x habitat (ridge)	-0.03	0.62	-0.05	0.962
Disturbance x habitat (snow bed)	0.87	0.62	1.39	0.169
Hjerkinn, *R^2 = 0.53*				
Intercept	2.82	0.31	9.12	<0.001
Severe disturbance	-0.19	0.43	-0.45	0.654

Ridge vs. leeside	-2.66	0.44	-6.08	<0.001
Snow bed vs. leeside	-0.36	0.43	-0.84	0.406
Disturbance x habitat (ridge)	0.26	0.61	0.43	0.668
Disturbance x habitat (snow bed)	0.06	0.60	0.10	0.921

*Table 9. Square root transformed abundance of graminoids as a function of treatment, habitat and site and interactions between treatment*habitat and treatment*site. Data pooled over site.*

Graminoids, $R^2 = 0.60$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	3.80	0.31	12.37	<0.001
Severe disturbance	-0.45	0.43	-1.05	0.295
Ridge vs. leeside	-3.24	0.37	-8.66	<0.001
Snow bed vs. leeside	-0.90	0.37	-2.44	0.016
Hjerkinn vs. Grødalen	1.94	0.30	6.43	<0.001
Disturbance x habitat (ridge)	0.44	0.52	0.84	0.405
Disturbance x habitat (snow bed)	0.11	0.52	0.21	0.831
Disturbance x site	-0.45	0.42	-1.06	0.289

*Table 10. Interactions of treatment*site on graminoid abundance in each habitat. Models for ridges and snow beds are square root transformed.*

Leeside, $R^2 = 0.27$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	20.55	2.81	7.30	<0.001
Disturbance x site	3.73	5.51	0.68	0.502

Ridge, $R^2 = 0.17$				
Intercept	0.74	0.32	2.28	0.028
Disturbance x site	-1.13	0.66	-1.72	0.094
Snow bed, $R^2 = 0.56$				
Intercept	2.32	0.36	6.37	<0.001
Disturbance x site	-0.53	0.73	-0.72	0.474

*Table 11. Square root transformed abundance of graminoids as a function of treatment, habitat and the interaction between treatment*habitat. Data separated by site.*

Grødalen, $R^2 = 0.46$	**estimate**	**standard error**	**t-value**	**p-value**
Intercept	4.23	0.38	11.05	<0.001
Severe disturbance	-0.87	0.53	-1.64	0.106
Ridge vs. leeside	-3.49	0.53	-6.59	<0.001
Snow bed vs. leeside	-1.91	0.53	-3.60	<0.001
Disturbance x habitat (ridge)	1.20	0.74	1.62	0.110
Disturbance x habitat (snow bed)	0.57	0.74	0.77	0.446
Hjerkinn, $R^2 = 0.65$				
Intercept	5.32	0.33	15.92	<0.001
Severe disturbance	-0.48	0.46	-1.04	0.305
Ridge vs. leeside	-3.01	0.47	-6.34	<0.001
Snow bed vs. leeside	0.10	0.46	0.22	0.829

Disturbance x habitat (ridge)	-0.31	0.65	-0.48	0.632
Disturbance x habitat (snow bed)	-0.35	0.65	-0.54	0.593

Table 12. List of species found in each site and control plots (A) and disturbed plots (C). Value is the sum of sub plot frequency for each species and sum of species count for each treatment at the bottom.

Site	**Grødalen**		**Hjerkinn**	
Treatment	**A**	**C**	**A**	**C**
	Sum. Sub plot frequency			
Agrostis mertensii	0	0	26	29
Fjellkvein				
Andromeda polifolia	2	20	0	0
Kvitlyng				
Antennaria alpina	0	0	1	0
Fjellkattefot				
Antennaria dioica	0	0	0	3
Kattefot				
Anthoxanthum nipponicum	35	25	124	129
Fjellgulaks				
Arctous alpinus	5	5	0	0
Rypebær				
Avenella flexuosa	124	64	166	152
Smyle				
Beckwithia glacialis	0	0	0	1
Issoleie				
Betula nana	111	40	107	42
Dvergbjørk				
Betula pubescens ssp. tortuosa	0	2	0	0
Fjellbjørk				
Bistorta vivipara	0	1	68	98
Harerug				
Calluna vulgaris	4	7	0	0
Røsslyng				
Campanula rotundifolia	0	0	4	7
Blåklokke				
Carex bigelowii	130	80	234	169
Stivstarr				
Carex lachenalii	0	1	24	20
Rypestarr				
Carex sp.	0	0	0	2

Starrslekta				
Carex vaginata	0	0	2	2
Slirestarr				
Cerastium cerastoides	1	0	25	2
Brearve				
Deschampsia alpina	5	0	0	0
Fjellbunke				
Deschampsia cespitosa	0	0	14	3
Sølvbunke				
Diapensia lapponica	8	2	0	1
Fjellpryd				
Diphasiastrum alpinum	49	11	18	7
Fjelljamne				
Empetrum nigrum ssp. hermaphroditum	338	205	134	69
Fjellkrekling				
Epilobium anagallidifolium	2	0	1	0
Dvergmjølke				
Eriophorum vaginatum	7	10	0	0
Torvull				
Euphrasia wettsteinii	0	0	7	15
Fjellaugnetrøst				
Festuca ovina	0	0	70	35
Sauesvingel				
Festuca rubra	0	0	7	3
Raudsvingel				
Harrimanella hypnoides	21	11	23	13
Moselyng				
Hieracium sec. alpina	3	3	15	25
Fjellsvæver				
Huperzia appressa	5	1	1	2
Fjell-lusegras				
Juncus trifidus	19	41	35	27
Rabbesiv				
Juniperus communis	0	0	16	1
Einer				
Leontodon autumnalis	0	8	0	14
Følblom				
Loiseleuria procumbens	104	79	25	6
Greplyng				
Luzula confusa	0	0	3	8
Vardefrytle				
Luzula multiflora	0	0	0	1
Engfrytle				
Luzula sp.	0	0	3	1
Frytleslekta				
Luzula spicata	0	3	10	3

Aksfrytle				
Minuartia biflora	0	0	0	1
Tuvearve				
Nardus stricta	2	8	5	5
Finnskjegg				
Omalotheca norvegica	0	0	0	3
Setergråurt				
Omalotheca supina	46	96	56	43
Dverggråurt				
Oxyria digyna	0	0	7	3
Fjellsyre				
Pedicularis lapponica	7	2	6	7
Bleikmyrklegg				
Phleum alpinum	0	0	5	0
Fjelltimotei				
Phyllodoce caerulea	54	20	98	44
Blålyng				
Pinguicula vulgaris	1	26	0	0
Tettegras				
Poa alpina	10	8	21	7
Fjellrapp				
Poa pratensis	0	0	11	7
Engrapp				
Pyrola minor	0	5	18	14
Perlevintergrønn				
Pyrola sp.	1	0	2	2
Vintergrønnslekta				
Ranunculus acris	0	0	0	1
Engsoleie				
Ranunculus pygmaeus	0	0	4	0
Dvergsoleie				
Rubus chamaemorus	1	0	0	0
Molte				
Rumex acetosa	0	0	4	4
Småsyre				
Sagina nivalis	0	0	0	9
Jøkulsmåarve				
Sagina sp.	0	0	0	2
Småarveslekta				
Salix herbacea	338	267	344	368
Musøyre				
Salix sp.	0	0	0	1
Vierslekta				
Saussurea alpina	0	0	22	12
Fjelltistel				
Saxifraga oppositifolia	0	0	0	4

Raudsildre				
Saxifraga stellaris	0	9	0	0
Stjernesildre				
Saxifraga tenuis	0	0	0	1
Grannsildre				
Sibbaldia procumbens	14	27	101	105
Trefingerurt				
Silene acaulis	0	0	0	1
Fjellsmelle				
Solidago virgaurea	2	3	29	13
Gullris				
Taraxacum croceum agg.	0	0	29	17
Fjell-løvetenner				
Thalictrum alpinum	0	0	3	2
Fjellfrøstjerne				
Trientalis europaea	0	0	10	7
Skogstjerne				
Vaccinium myrtillus	249	186	96	137
Blåbær				
Vaccinium uliginosum	25	47	38	4
Blokkebær				
Vaccinium vitis-idaea	158	166	122	145
Tyttebær				
Veronica alpina	0	0	47	38
Fjellveronika				
Viola palustris	3	20	0	4
Myrfiol				
Sum. Species	**34**	**36**	**50**	**62**