

Long-term Exclusion of Mammalian  
Herbivores Affect Plant Biomass in Plant  
Communities of the Tundra in Northern  
Norway  
by  
Karolina Norrman



# Plants & Ecology

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Department of Botany  
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Plant Communities of the Tundra in  
Northern Norway

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Cover: *The ground vegetation consisting of lichens (Cladonia) and mosses in the study area in northern Norway.*

## **Abstract**

Unproductive ecosystems like tundra and steppes, has short growing season and low plant productivity, factors that makes the mammalian herbivores in the area resource limited. Due to limitation in food, herbivores impact on the plant population can be massive as they consume everything they can. Studies have shown that different intensities of herbivory affect plant biomass, abundance and diversity, by removing biomass and with that changing the balance of competition among plants, herbivores control plant communities.

This study is based on three different studies with the starting time of 1988, 1998 and 2007. The aim was to make a long-term study of how the biomass in unproductive areas responds to exclusion of mammalian herbivores by measuring changes in plant biomass. The study was conducted in snow bed heaths on a highland plateau in Finnmarksvidda in northern Norway. Exclosures and controls had been put up in 1988, 1998 and 2007, and during the summer of 2008, all living biomass was collected, sorted into species or genus and dried. In this study, a total number of 22 exclosures and 42 controls were used from the three different studies. The result show that plant biomass is affected by exclusion of mammalian herbivores, where higher amounts are found in the exclosures, and that the biomass is decreasing with time. Since no interaction was found between exclosure and time, the conclusion drawn from this study are that long-term exclosures seems to affect plant biomass in unproductive areas differently than short-term exclosures.

## **Sammanfattning**

I lågproduktiva ekosystem, exempelvis tundra och stepp, är den korta växtsäsongen och den låga växtproduktiviteten faktorer som begränsar resurserna för de växtätande däggdjur som finns i området. På grund av att den tillgängliga födan är begränsad kan växtätarnas påverkan på växtpopulationen vara mycket stor då de under kort tid konsumerar så mycket som möjligt. Studier har visat att olika intensiteter av bete påverkar växtbiomassa, täthet och diversitet. Vid bete försvinner biomassa och därmed ändras den naturligt rådande balansen mellan konkurrerande arter. På så vis kontrolleras växtpopulationen av växtätare.

Den här studien baseras på tre olika studier med startår 1988, 1998 och 2007. Målet var att göra en långtidsstudie om hur biomassa i lågproduktiva områden påverkas vid uteslutning av växtätande däggdjur genom att mäta förändringar i biomassan hos växter. De tre studierna utfördes i snölegor på en höglandsplatå i Finnmarksvidda i nordligaste Norge. Inhägnader och kontroller sattes upp 1988, 1998 och 2007 och under sommaren 2008 samlades all biomassa in och sorterades på art- eller släktnivå. Totalt användes 22 inhägnader och 42 kontroller från

de tre olika studierna.

Resultaten visar att växtbiomassan påverkades när växtätande däggdjur utesluts och större mängder biomassa återfinns i inhägnaderna. Växtbiomassan minskar även signifikant med tiden under de 20 år som studien baseras på. Även om ingen interaktion mellan inhägnad och tid hittades, tycks det föreligga en skillnad (Fig. 2) och då signifikantsnivån var väldigt låg (Table 1), blir slutsatsen av denna studie att biomassan hos växter tycks påverkas olika vid kort respektive lång uteslutning av växtätande däggdjur.

## **Introduction**

Unproductive ecosystems, like tundra and steppe, with short and comparatively cool growing seasons and low plant productivity, make herbivore populations in these areas strictly resource limited (Carlsson et al., 1999). Because of the food limitation, herbivores' impact on the plant population can be massive, as they may deplete the vegetation when consuming everything they can (Oksanen et al., 1997, Oksanen & Oksanen, 1981). Numbers of studies conducted in unproductive ecosystems during the last decades have shown that different intensities of herbivory have considerable impact on plant biomass, abundance and diversity (Olofsson et al., 2002, Olofsson et al., 2004, Grellman, 2002, Virtanen et al., 1997, Austerheim & Eriksson, 2001, Lindgren, 2007, Bonser & Reader, 1995 and Brathen & Oksanen, 2001). By removing biomass and with that changing the balance of competition among plants, herbivores control plant communities (Mulder, 1999), while plant species diversity depend not only on the intensity and the frequency of grazing but also on type of grazer (Hobbs & Huenneke, 1992).

An area where the plant communities are strongly controlled by grazing are the Scandinavian mountains (Austerheim & Eriksson, 2001) where the mammalian herbivores constitute mainly of rodents and reindeers. Since rodents often are constantly present in the area, their effect on the mountain heath vegetation is higher than the effect by reindeers, that only graze during parts of the year in the same area (Olofsson et al., 2004, Olofsson et al., 2004, Gutiérrez et al., 1997, Moen & Oksanen, 1998).

Except for increased herbivory, that has been showed to decrease the intensity of plant competition (Olofsson et al., 2002), plant communities are also shaped by direct and indirect interactions (Olofsson et al., 2002, Oksanen & Virtanen, 1995b). The interactions occur not only between individuals of the same plant species, but also between individuals from different species (Bazzaz, 1990). Earlier studies indicate that plant competition increases with increased biomass (Olofsson et al., 2002, Oksanen & Virtanen, 1995b) while other studies

indicate the opposite.

Exclosure studies conducted in Serengeti, Tanzania, show that the replacement of short grasses by tall grasses occurs more rapidly without the presence of herbivores (McNaughton, 1979). The same observations have been done in exclosure experiments on the tundra in northern Norway where the tallest and most broad-leaved plants were favored (Oksanen & Oksanen, 1981, Oksanen, 1990). Without herbivory in snowbed heaths it is conceivable that higher herbs will out-compete smaller species and the decrease in soil nutrient will benefit the spread of trailing herbs (Oksanen & Moen, 1998, Oksanen & Moen, 1994, Stark et al., 2002, Oksanen & Moen, 1994). Grasses are another plant group that has shown to be benefited by long-term exclosures on the cost of mosses and lichens that may still be present in high amounts (Virtanen, 2000).

In strongly grazed areas, plant success depends on the ability to sustain grazing better than their neighboring plants (Oksanen & Virtanen, 1995b). There are two different strategies for plants to cope with mammalian herbivory. Either the plants protect themselves from being grazed or they are adapted to sustain grazing. For example, graminoids are poorly defended against herbivores but have a rapid regrowth whereas evergreen shrubs are heavily defended against herbivores but have a poor regrowth (Oksanen, 1990). The increased nutrient availability in the soil due to herbivore feces benefits vascular plants as herbs and grasses that out-compete both mosses and lichens (Tömmervik et al., 2004, Grellmann, 2002). Studies have shown that rodents are able to graze 40-60% of the total amount of vegetation underneath the snow (Virtanen et al., 2002). Since herbs save their resources in vegetation parts above ground, herbivory during winter time are more severe for shrubs compared to grasses (Hambäck & Ekerholm, 1997). In a study where grasses were consumed most, they also recovered best and one and a half year later the amount had increased partly due to reduced plant competition and increased nutrition through feces (Moen et al., 1993a, Emanuelsson, 1984a, Kryazhimskii & Danilov, 2000).

The effects on plant communities in absence of mammalian herbivores have been studied quite many times but these studies have mostly been short-term studies for about three to seven years. Since plant communities are affected by so many factors, the effects can probably not be seen immediately and therefore it is possible that short-term studies might give an incomplete or incorrect picture of herbivores effect on plant communities.

The purpose of this study was to examine how the vegetation in the unproductive areas of the Fennoscandian tundra responds to the removal of grazers by measuring changes in biomass. By collecting biomass from exclosures that were put up on snowbed heaths one year, ten

years and two decades ago, long-term enclosure effects on biomass changes in plant communities were possible to be studied. All plant species were categorized into one of the six plant groups' herbs, mosses, lichens, graminoids, evergreen or deciduous plants that was used in this study.

According to earlier studies, plant biomass is expected to increase in areas without mammalian herbivores. Due to this fact, the biomass in the treatments for especially competitive plant groups as grasses and herbs, are expected to be higher in the older studies (1988 and 1998) compared to the youngest (2007) and controls, where the plants still not yet have recovered from being grazed. The absence of herbivores will lead to increased plant competition that will result in lower plant diversity. Competitive vascular plants as grasses and herbs will dominate at the cost of other plant groups, as mosses and lichens that are expected to decrease in biomass in the older studies (1988 and 1998).

## **Method**

### *The study area*

The study area is located on a highland plateau at 600 m a.s.l. near the lake Joatkanjávri/Stuorajávri (69°45'23''N, 23°54'40''E) in Finnmarksvidda in northernmost Norway. The area belongs to the arctic zone with a characteristically short growing season that starts at the end of June and lasts until the beginning of September. Due to the continental climate in the area, the temperature varies a lot between summer and winter and the precipitation is poor (Oksanen, 1997).

Lichen heaths and graminoids dominate the tundra heath vegetation (Oksanen & Virtanen, 1995a & 1995b, Carlsson et al., 1999). Characteristic vascular plants in the area are *Salix herbacea*, *Vaccinium myrtillus*, *V. vitis-idea*, *Trientalis europaea* and *Carex ssp.*, while *Kieria*, *Cladonia*, *Polytrichum* and *Cladina* are the most common moss and lichen genera. The study was conducted in snow bed heaths consisting of mainly graminoids, small herbs, lichens and mosses. The diversity in snow bed heaths is usually high and the species are adapted to relative high winter temperatures, short growing season (ca. 40-60 days) and low plant competition. Since the snow beds melt later than the surroundings the vegetation is longer protected from herbivory by reindeers while rodents, that live and move underneath the snow, has a bigger impact.

### *Mammalian herbivores in the area*

The Fennoscandian tundra and mountain range is mostly grazed by reindeers (*Rangifer tarandus*) and rodents. Migrating reindeers mainly occur in the study area during spring

(April/March) and autumn (September/October) migrations, but low numbers of reindeer can be found in the area throughout the summer were they consume mostly grasses and leaves. Herbivory by reindeers have been shown to change the plant species composition as well as the primary production (Olofson et al., 2001, Värde et al., 1995). Grasses are one group that benefit from reindeer presence while both trampling and grazing affect mosses and reindeer lichens (*Cladina rangiferina*) negatively (Olofson et al., 2001, Stark et al., 2002, Van der Wal & Brooker, 2004, Värde, 2001, Den Herde et al., 2003). Between 1980 and 1990 there was a high abundance of reindeers on Norwegian Finnmarksvidda (Tømmervik et al., 2004).

The most common rodent is the grey-sided vole (*Clethrionomys rufocanus*) which is regularly found in the area (Hambäck et al., 2002, Oksanen, 1997). The diet of grey-sided voles varies and during summer they eat mostly herbs, while dwarf shrubs and dicotyledonous plants such as bilberry (*Vaccinium myrtillus*), preferentially shoots, are their main food resource wintertime (Kalela, 1957). The vole population density varies with three to four years cycles probably due to a combination of mustelid predation and food availability (Oksanen & Oksanen, 1992, Hambäck et al., 1998). During the enclosure study, vole peaks occurred in 1987/88, where the population only reached moderate densities (Moen et al., 1993), and in 1992/93 (Hambäck et al., 2002).

At higher altitudes the Norwegian lemming (*Lemmus lemmus*) is abundant and consumes mainly mosses and graminoids (Mulder, 1999). As for grey-sided voles, the lemming population is nothing but constant. During peak years, the population increases rapidly and large amounts of available food are consumed (Kalela et al., 1971). Due to yet unestablished factors, among other lack of food resources (Oksanen & Oksanen, 1981), there is a rapid decline of the population number. Between the peaks, that occur approximately every tenth year, lemmings are almost absent (Kalela et al., 1971, Oksanen & Oksanen, 1981, Moen et al., 1993). During this study period, lemming outbreaks occurred in 1987/88 and 2007/08 and regular trapping showed that only low numbers of lemmings were present between the population peaks.

### *Experimental design*

This study compared three different studies with starting year of 1988, 1998 and 2007, respectively, and thus includes enclosure studies with the lengths of 20 years, 10 years and one year. The studies were distributed among five study areas within similar habitats of tundra and snow bed heaths on the highland (Fig. 1).

### *The study from 1988 – 20 years old*



During the summer of 1988, during a lemming outbreak, Jon Moen established 24 plots (50x80 cm, we used 50x50 cm) in area D (Fig. 1) where half of the plots were fenced by galvanized net. The exclosures had a size of 80x120 cm and a height of 60 cm. The net was dug down approximately 15 cm into the soil and snap-traps were put inside (during the experiment no animals were caught) (see Moen et al., 1993). Out of 12 exclosures, only five seemed to be intact after 20 years and could be used in this study.

#### *The study from 1998 – 10 years old*

In 1998, Johan Olofsson established 20 plots (50x50 cm) randomly spread in areas A, B, C and D on the tundra heath (Fig. 1). The criteria used for the selection of the study areas were homogeneous areas with snow bed (heath vegetation) containing *Salix herbacea* or other species that indicate late snow melting. In areas A and B, three pairs of square plots (two pairs in areas C and D) were spread out close to each other where one plot within each pair was randomly allocated to exclosure. To keep reindeers and rodents out, a galvanized net was used. Each exclosure was 80x120 cm large, had a height of 80 cm and fences were dug about 15 cm into the soil. During ten years, the fenced areas were not exposed to grazing by any mammalian herbivores. Until summer 2008, three fenced plots had been destroyed by four wheel vehicles and could not be used and therefore only seven pairs, two each in areas A, B and D and one in area C, were used in this study.

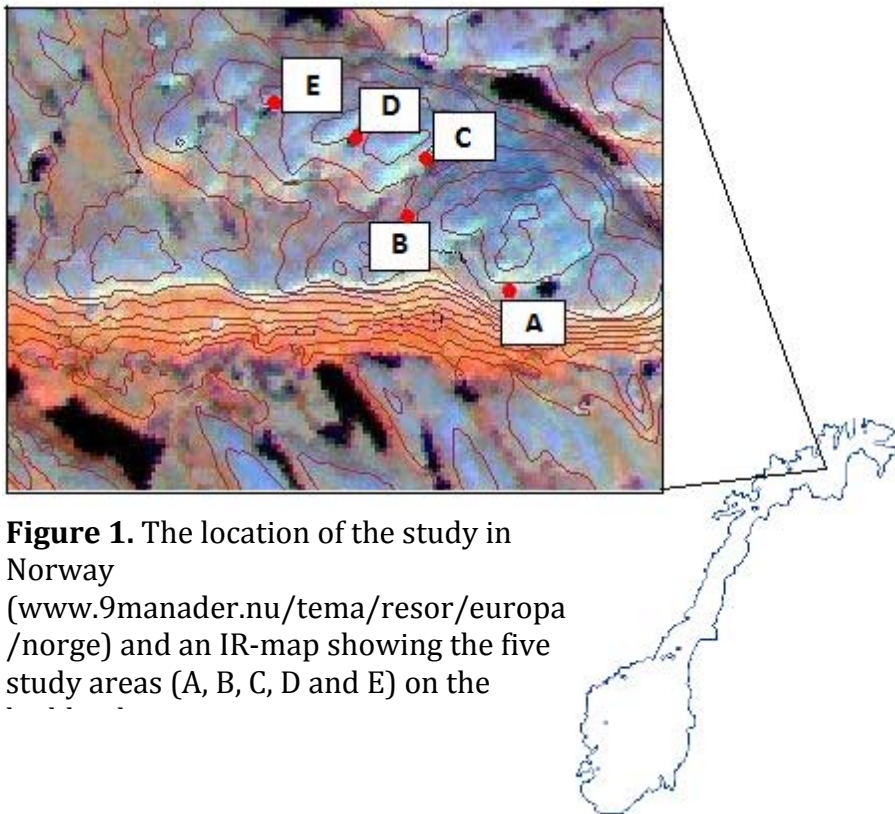
#### *The study from 2007 – one year old*

During the summer 2007, 20 plots (25x25 cm) were established and spread out randomly in two areas, D and E (Fig. 1). Half of the plots were randomly allocated as herbivore exclosures and were fenced with a galvanized net. Compared to the older studies, this study had a different design. Similar to a hat, the net covered the exclosure like a roof and a thick plastic had been nailed in to the soil around and over the net edges to prevent rodents from entering. In addition, biomass from 10 extra control plots in each area was collected to increase the number of data points.

#### *Sampling - summer 2008*

During the two first weeks of August, all living vegetation inside the 64 plots (50x50 and 25x25 cm) were cut above-ground and one cm down in to the soil. Vegetation that was dead but still had living parts, even if the living parts were outside the fenced area, were cut and collected. All dead vegetation in the plots was excluded. For the sampling of mosses and lichens a circular object with a diameter of 7.5 cm was used to cut out six patches from the vegetation carpet according to the following directions (randomly chosen) for areas A, B, C and D (studies 1988-2008 and 1998-2008): 4 cm N, 20 cm NE, 16 cm E, 8 cm S, 12 cm W

and 16 cm NW from the middle point of each area. Since the plots in areas D and E (study 2007-2008) were only one quarter of the size of plots in the other areas, only three patches was cut out with half of the length randomly chosen according to the following directions: 2 cm S, 8 cm NE and 10 cm NW from the middle point of each plot. The biomass was sorted in the field to species or genus (nomenclature follows Lid, 1985). To group the different plant species, six different plant groups were used: evergreen plants (e), deciduous plants (d), graminoids (g), herbs (h), mosses (m) and lichens (l). All the samples were dried for at least 24 hours in a vacuum desiccator with one kilogram silica.



**Figure 1.** The location of the study in Norway ([www.9manader.nu/tema/resor/europa/norge](http://www.9manader.nu/tema/resor/europa/norge)) and an IR-map showing the five study areas (A, B, C, D and E) on the

### *Statistical method*

The biomass data was first corrected for sampling area (the biomass in the analysis in all cases is per one square meter ( $m^2$ )). All biomass data was log-transformed to normalize error distributions and to equalize variances. All the data was analyzed with the statistical program R 2.8.1.

The relationships between biomass ( $\log g/m^2$ ) depending on treatment (fenced) and time (1988-2008, 1998-2008 and 2007-2008) were tested with 2-way ANOVA.

To see how the biomass for the six different plant groups (herbs, graminoids, deciduous, lichens, mosses and evergreen plants) were affected by the absence of herbivores during the different time-scales (1988-2008, 1998-2008 and 2007-2008), the data was analyzed with

ANOVA.

Pie charts were used to get a relative proportion of the biomass distribution for the six plant groups in the exclosures and the controls for the three different studies (1988-2008, 1998-2008 & 2007-2008). No statistical tests were made.

## Results

### *Biomass changes due to exclosures of mammalian herbivores*

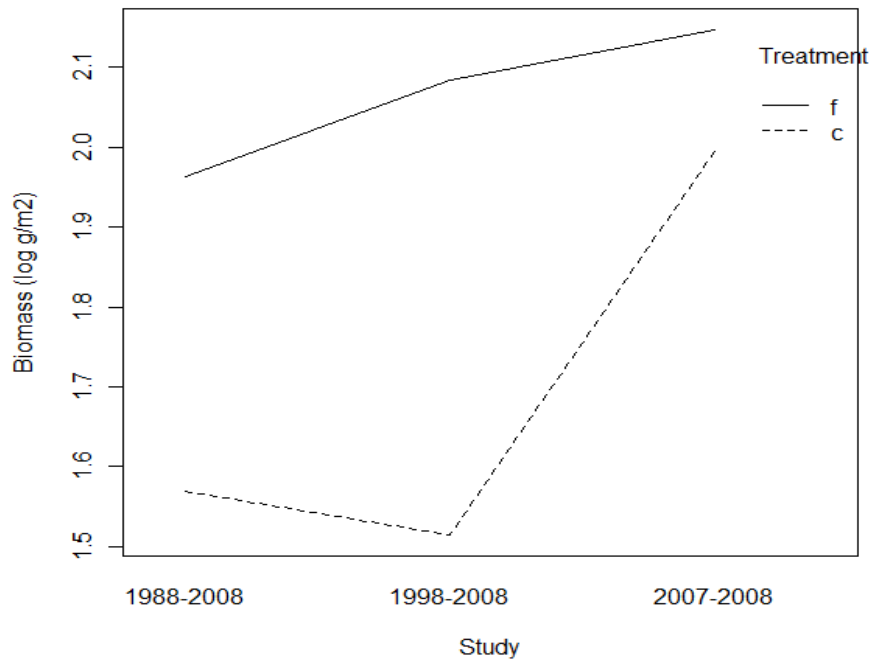
Strong significant relationships were found between the amount of biomass and treatment (fenced) and between biomass and time (the three different studies) (Table 1 & Fig. 2). Since no interaction between study/time and fence was found, no differences in the effect from the absence of herbivores between the three studies (time) was seen.

**Table 1.** ANOVA table of the biomass for the three studies (1988-2008, 1998-2008 and 2007-2008) and treatment (fenced).

		Df	Sum Sq	Mean Sq	F-value	Pr (>F)
<b>Time/study</b>	2	0,918	0,457	6,017	<b>0,0042**</b>	
<b>Fence</b>	1	1,263	1,263	16,558	<b>0,00014 ***</b>	
<b>Interaction</b>	2	0,437	0,219	2,866	0,0650	
<b>Residuals</b>	58	4,424	0,0763			

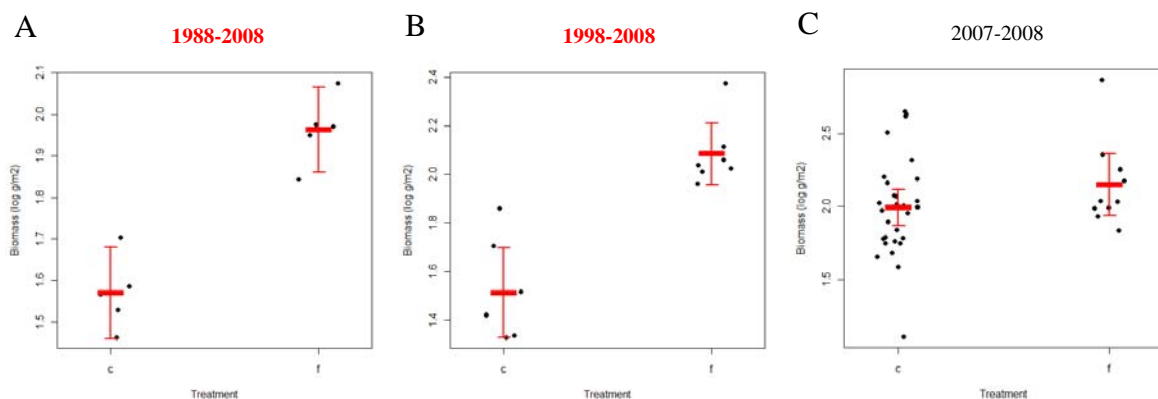
Significant levels: 0,05 (\*), 0,001 (\*\*), and 0,0001 (\*\*\*)

Over all, in all the three studies the biomass was higher in the treatments compared to controls (Fig. 3). A decline in biomass with the age of the study (time) could be seen, which was the opposite of the hypothesis. While the biomass in the oldest treatment (1988-2008) was lower compared to the 10 year old exclosure (1998-2008), the opposite pattern was observed for the controls (Fig. 2). The highest difference in biomass was seen between the exclosure and the control of the study 1998-2008 while the smallest was found in the study 2007-2008 (Fig.2).



**Figure 2.** The relationship between biomass ( $\log (\text{g}/\text{m}^2)$ ), study (1988-2008, 1998-2008 and 2007-2008) and treatment (fence (f) and control (c)).

Looking at each study separately, the relationship between biomass and treatment for each of the three studies was analyzed with one-way ANOVA. Strong significant relationships were found for the 10 years old ( $p < 0,001$ ,  $SS = 1,14$ ,  $F\text{-value} = 38,73$ ) (Fig. 3 B) and 20 years old ( $p < 0,001$ ,  $SS = 0,39$ ,  $F\text{-value} = 52,64$ ) (Fig. 3 A) studies but not for the one year old study (Fig. 3 C).



**Figure 3.** The relationship between biomass ( $\log (\text{g}/\text{m}^2)$ ) and treatment (fence (f) and control (c)), with mean and variation for each of the three studies (1988-2008, 1998-2008 and 2007-2008), compared to controls. Not different scales.

### *Biomass changes in each of the six plant groups*

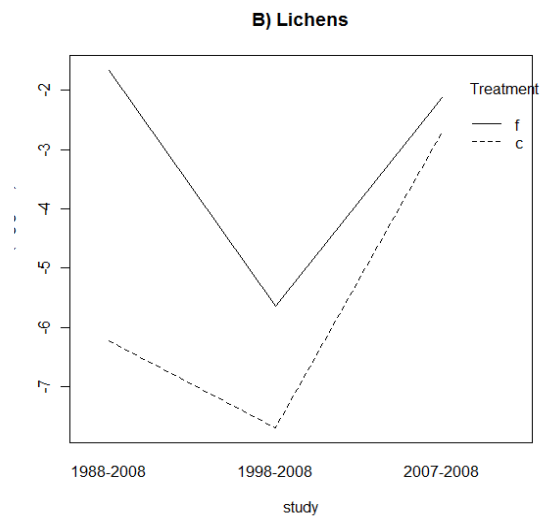
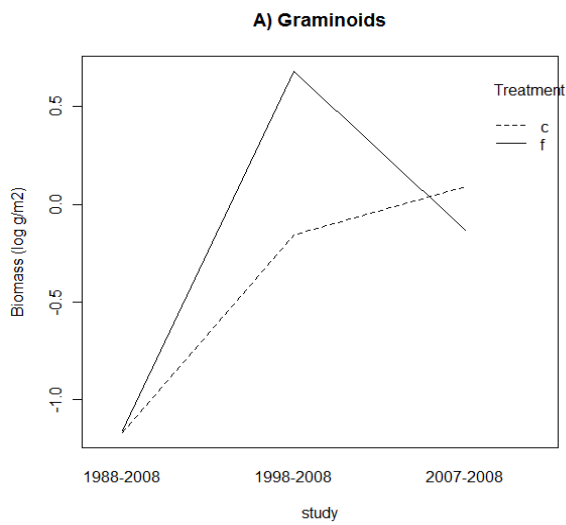
The results show that only the absence of mammalian herbivory did not significantly affect the biomass for any of the plant groups when analysed separately. However, when looking at the time-perspective (studies), significant results were found for graminoids ( $p < 0,05$ ), mosses ( $p < 0,0001$ ) and lichens ( $p < 0,05$ ) (Table 2 and Fig. 4 a,b & c) but not for the groups herbs, deciduous and evergreen plants (Table 2 and Fig. 5 d,e & f). For the plant group lichens, an interaction between time (study) and treatment (fenced) was found ( $p < 0,05$ ), indicating that the effect from the absence of herbivores differs among the three different studies (time). In the study 2007-2008, the plant groups lichens, mosses and deciduous plants gained from the absence of mammalian herbivores, resulting in a higher biomass in the exclosures (Fig. 4 b, c & 5 e). While both mosses and deciduous plants decreased in biomass with time, the plant group lichens increased in biomass (Fig. 4 b, c & 5 e). The biomass in both exclosure and controls for the three plant groups was lower in the study 1998-2008 compared to the 2007-2008 study. However, in the study 1998-2007, only the mosses had a lower biomass in the exclosures compared to the controls (Fig. 4 c). Even though the biomass for mosses in the exclosures was almost unchanged in the oldest study (1988-2008) compared to the levels in the study 1998-2008, the biomass in the exclosure was higher than in the controls for this year (Fig. 4 c). The biomass for lichens and deciduous plants was higher in the study 1988-2008 than in the 1998-2008 study, creating a V-shaped pattern where the biomass change in the exclosure and the controls through out the three studies looked almost the same (Fig. 4 b & 5 e). Even though the difference in biomass levels between exclosure and control for lichens was high in the study 1988-2008, the difference was not significant (Fig. 4 b). In the study 2007-2008, the biomass for the plant groups graminoids, herbs and evergreen plants were all lower in the exclosures than in the controls (Fig. 4 a, 5 d & f). While the biomasses in the exclosures for all the three groups were higher than in the controls in the study 1998-2008, the biomasses were also higher compared to the exclosures in the study 2007-2008 (Fig. 4 a, 5 d & f). For the group graminoids, there was no difference in biomass between the exclosures and controls in the oldest study (1988-2008) (Fig. 4 a). The biomass for evergreen plants was lower in the exclosures of the study 1988-2008 than in both 1998-2008 and 2007-2008, however, still reaching higher levels than in the controls (Fig. 5 f). Only for the plant group herbs did the biomass in the exclosure increase with the age of the study, reaching the highest biomass in the oldest study (1988-2008) (Fig. 5 d). Compare this to the controls, where the lowest biomass of herbs was observed in the study 1998-2008 (Fig. 5 d).

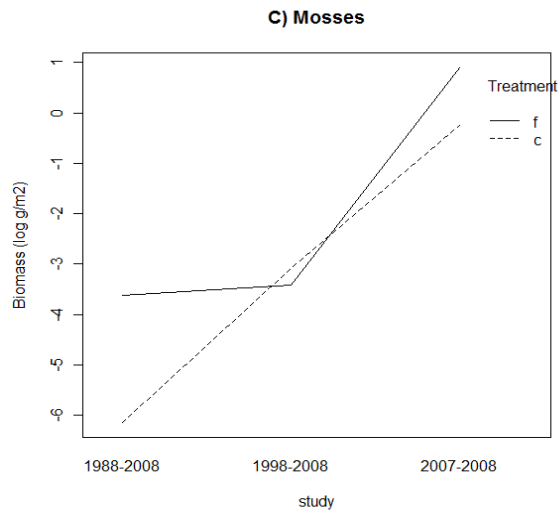
**Table 2.** F-values and p-values from ANOVA for the six different plant groups for treatment,

study/time and interaction.

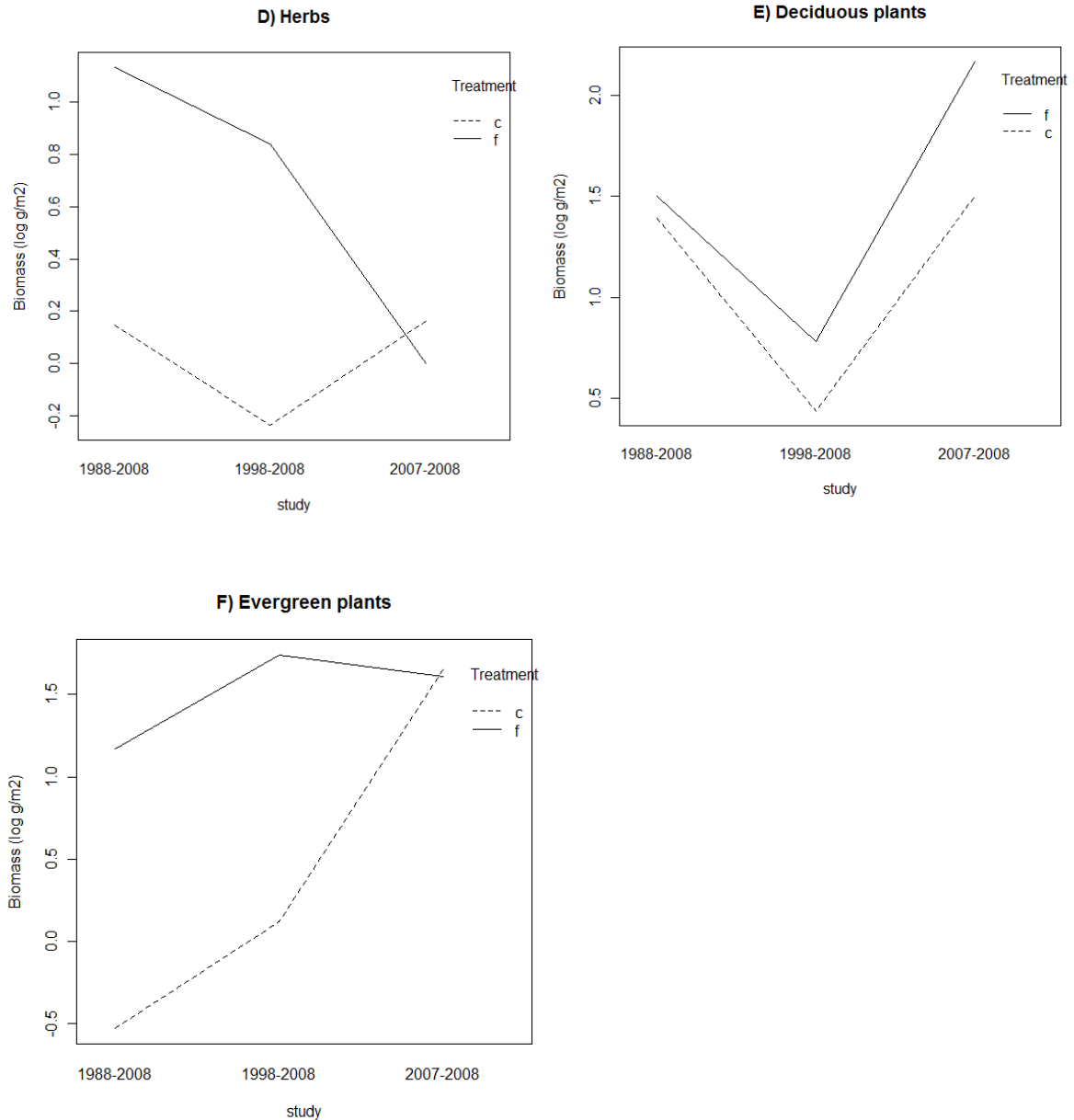
	Fenced	(Pr (>F))	Time/Study	(Pr (>F))	Interaction	(Pr (>F))	Error (MS)
<b>Deciduous pl.</b>	1,781	(0,187)	1,826	(0,182)	0,217	(0,643)	1,14
<b>Evergreen pl.</b>	1,992	(0,165)	2,909	(0,095)	3,297	(0,076)	1,89
<b>Graminoids</b>	0,574	(0,453)	5,974	<b>(0,019*)</b>	0,491	(0,487)	0,82
<b>Herbs</b>	1,140	(0,290)	0,660	(0,420)	2,939	(0,092)	1,74
<b>Mosses</b>	0,808	(0,184)	39,04	<b>(4,99e-08***)</b>	0,315	(0,577)	6,18
<b>Lichens</b>	1,991	(0,164)	5,443	<b>(0,023*)</b>	4,020	<b>(0,050*)</b>	9,02

Significant levels: 0,05 (\*), 0,001 (\*\*), and 0,0001 (\*\*\*)





**Figure 4 a, b & c.** The relationship between biomass (log g/m<sup>2</sup>) and time/study (1988-2008, 1998-2008 and 2007-2008) for the treatment (f) and control (c) for the plant group graminoids, lichens and mosses. Not different scales.



**Figure 5 d, e & f.** The relationship between biomass (log g/m<sup>2</sup>) and time/study (1988-2008, 1998-2008 and 2007-2008) for the treatment (f) and control (c) for the plant groups herbs, deciduous and evergreen plants. Not different scales.

### *Plant group distribution*

To get a different view of how the biomass had changed with time and differed between enclosures and controls for the three studies (1988-2008, 1998-2008 and 2007-2008), the biomass in relative proportions of the six different plant groups was calculated presented in pie-charts (Fig. 6, 7 & 8).

When comparing the enclosures with the controls for the study 2007-2008 (Fig. 6), the

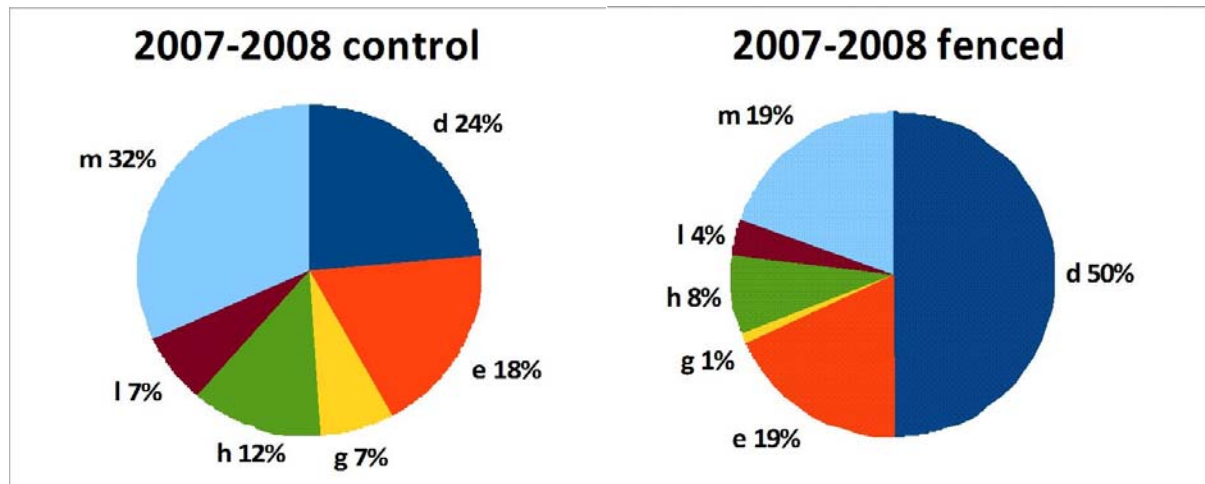


dominating plant species were evergreen (e), deciduous plants (d) and mosses (m), which were the same as in the controls. While the biomass proportion for the deciduous plants (d) was greater in the enclosure, the opposite pattern was found for mosses (m) while it for the evergreen plants (e) was almost unchanged. For herbs, graminoids and lichens the biomass proportion was smaller in the enclosures compared to controls.

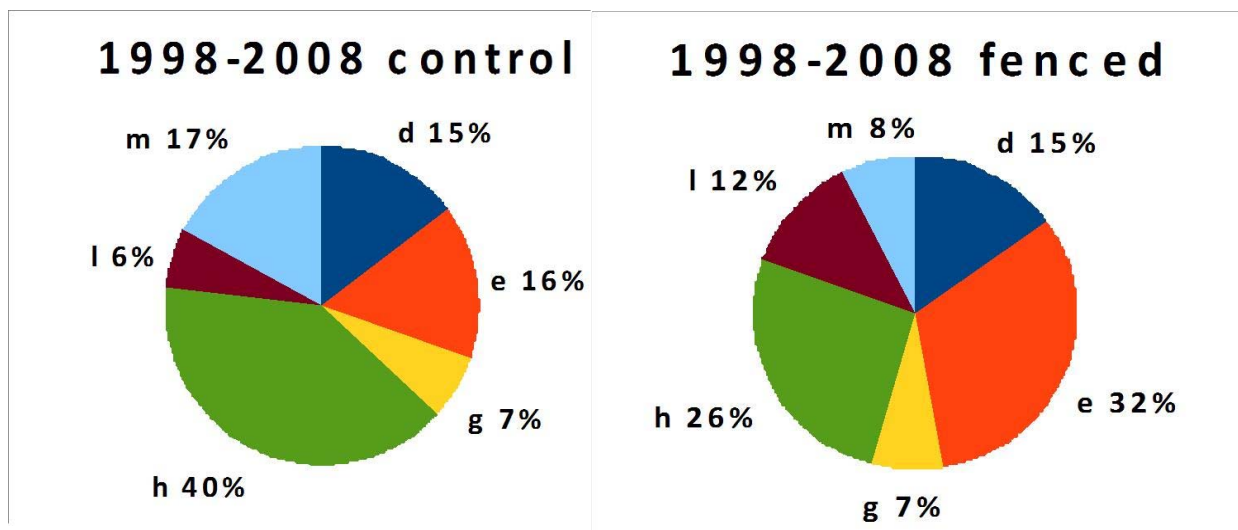
For the 1998-2008 study (Fig. 7), herbs (h) had dominated the biomass proportion in the controls. In the enclosures, the biomass proportion for herbs (h) was lower, while it for the evergreen plants (e) was higher than in the controls. The biomass proportion for graminoids (g) and deciduous plants (d) was unchanged. While the biomass proportion for mosses (m) was lower in the enclosures, constituting the second smallest plant group, the opposite pattern was observed for lichens (l).

Comparing the enclosures with the controls for the study 1988-2008 (Fig. 8), the biomass proportion was more even. Deciduous plants (d) that had dominated the controls with more than 80% of the total biomass proportion, was lower in the enclosures, constituting almost half the biomass proportion. All the other plant groups ((e), (g), (h) and (l)) , except for mosses (m), had a higher biomass proportion in the enclosures, where both evergreen plants (e) and lichens (l) had gained most.

When comparing the biomass proportion in the enclosures of the six different plant groups with every single study (2007-2008, 1998-2008 and 1988-2008) (time), mosses (m) was the only plant group that lost in biomass proportion throughout the twenty years. Lichens (l) gained in biomass proportion with the age of the study (time), while the other plant groups (evergreen, deciduous, herbs and graminoids) did not show any clear patterns of the changes in biomass proportion due to the excluded mammalian herbivores.

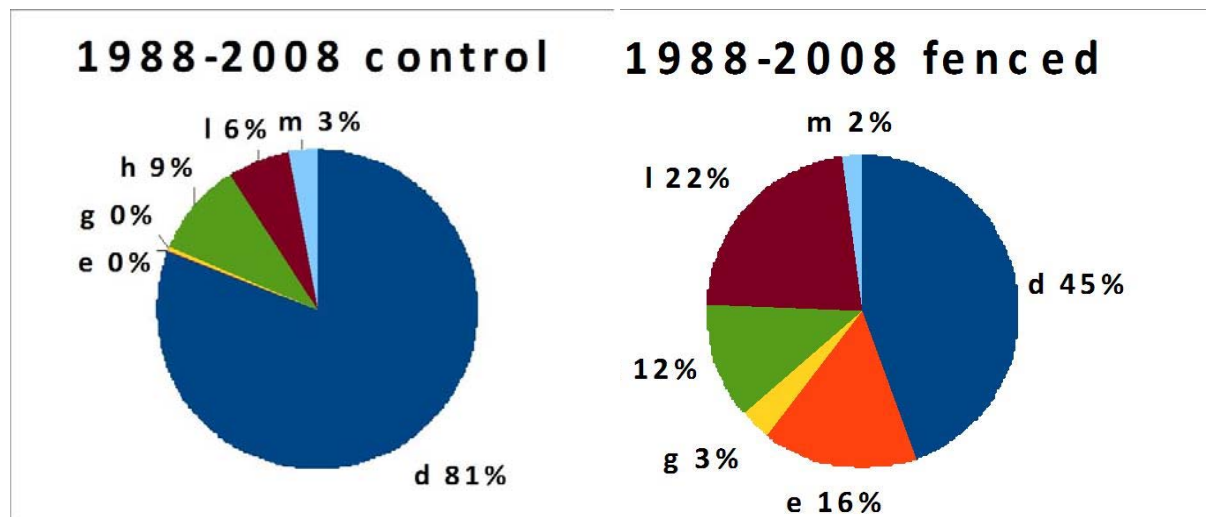


**Figure 6.** The proportion of the total biomass for each of the six plant groups for the controls



and fences of the study 2007-2008.

**Figure 7.** The proportion of the total biomass for each of the six plant groups for the controls and fences of the study 1998-2008.



**Figure 8.** The proportion of the total biomass for each of the six plant groups for the controls and fences of the study 1988-2008.

### Discussion

Not unexpectedly, and according to the main hypothesis, the plant biomass in the snow beds increases when mammalian herbivores are excluded. The time (the three different studies) has also a significant effect on the plant biomass where the biomass decreases with time, ending up with the lowest biomass in the oldest study (1988-2008). One possible reason for this could be plant competition that increases when the plant biomass increases (Olofsson et al., 2002, Oksanen & Virtanen, 1995). Since no significant interaction is found between treatment and time, the effect from the exclosures on the biomass is the same irrespective of the time and the biomass change is similar in all the three different studies (Table 1).

The rather lower biomass in the controls for the 1988-2008 and the 1998-2008 studies can perhaps be explained by the population peaks of lemmings (1987/88) (Moen et al., 1993) and voles (1987/88 and 1992/93) (Hambäck et al., 2002) that occurred during this time and the higher abundance of reindeer between 1980 and 1990 in this area (Tömmervik et al., 2004). One factor that can have affected the plant biomass in the exclosures of the study 1988-2008 is that the exclosures were put up when some grazing already had been taking place during the peak 1988 (Moen et al., 1993).

When testing the exclosures effect on the plant biomass for the three studies separately (Fig. 3), a significant relationship was found for both of the two oldest studies (1988-2008 and 1998-2008), while no significant effect was found for the youngest study (2007-2008). In November 2007, most of the snow in the area of the study 2007-2008 melted and soaked the

vegetation. Water, that when the temperature went down, froze, making the vegetation inaccessible for the mammalian herbivores, above all for the lemmings. This could be one reason for the quite high biomass levels that is seen in the controls for this year (2007-2008). Another reason for that the two oldest studies showed on significant results, could be that the biotope gradient/habitat is slightly different for the study 2007-2008 compared to the 1988-2008 and the 1998-2008 studies, where the exclosures for the 2007-2008 study were more dispersed and had less pronounced snow heath character. The fact that the different areas (A, B, C, D and E) were not exactly identical and other external factors could also explain the lower plant biomass in 1998-2008.

Even though quite big differences in biomass are seen between exclosures and controls, the biomass is not significantly affected by the exclosures for any of the six different plant groups (Table 2 & Fig 4 & 5). A larger sample size might have given other results, since the exclosures affects the total plant biomass when the plant groups are not separated. However, the biomass for the plant groups mosses, lichens and graminoids are significantly affected by time, where the biomass in the long run decreased with time for both mosses and graminoids, while it increased for lichens. The plant group lichens are clearly gaining from being excluded from mammalian herbivores, increasing in both relative and absolute biomass (Compare Fig. 6, 7 & 8) (Fig. 4 A), compared to controls, in all the three studies. One reason for the biomass increase could be that all other plant groups, except for herbs, are decreasing with time, resulting in lowered plant competition and increased availability of space. The interaction between treatment and time was only significant for lichens, indicating that there was a difference in the effect from the fence on the biomass for the three different studies.

As seen in the pie-chart for the exclosure of the oldest study (1988-2008), the biomass proportions for the six plant groups is quite even, all plant groups are represented in higher or smaller amounts, with lichens being one of the plant groups with largest biomass proportion. For controls in the same study, deciduous plants are clearly dominating the plant diversity and both graminoids and herbs are present with less than one percent, which support the statement that herbs and graminoids are favoured by mammalian herbivores (Virtanen, 2000, Tömmervik et al., 2004, Grellmann, 2002).

The biomass for most plant groups shows large variations between the studies (Fig. 4 & 5). For example, graminoids are gaining in biomass during ten years of exclosure (between the study 1998-2008 and 2007-2008)(Virtanen, 2000, Oksanen & Moen, 1998, Oksanen & Moen, 1994, Stark et al., 2002, Oksanen & Moen, 1994) but after another ten years (1988-2008 and 1998-2008), the biomass is decreasing. If the study had only been ten years long, only half of

the pattern would have been seen and other conclusions might have been drawn. This pattern shows the importance of long-term studies when studying plant communities since so many factors are determining and affecting the biomass.

The conclusion drawn from this study is that the ecological factors affecting the plant community structure in the Arctic areas is rather complex question, and affected by many factors, not only mammalian herbivory, that is well-known for having a big impact on plant communities in the Scandinavian mountains (Austrheim & Eriksson, 2001). For instance, interspecific plant competition is one of the additional factors that affect the plant community composition. Since no interaction was found between time and treatment, even though there seems to be a difference (Fig. 2) and the p-value was quite low (Table 1), the main conclusion drawn is that long-term exclusions seem to affect changes in biomass differently than short-term exclusions.

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## **Appendix**

### List of plant species

#### GRAMINOIDS

*Agrostis mertensii* (Fjällven)  
*Anthoxanthum odoratum* (Vårbrodd)  
*Deschampsia flexuosa* (Kruståtel)  
*Festuca ovina* (Fårsvingel)  
*Vahlodea artropurpurea* (Lapptåtel)

#### MOSSES

*Anastrophyllum* sp.  
*Aneura* (Bålmossa)  
*Aulacomnium turgidum* (Fjällräffelmossa)  
*Barbilophozia* sp. (Flikmossa)  
*Dicranum fuscescens* (Bergkvastmossa)  
*Dicranum majus* (Stor kvastmossa)  
*Dicranum scoparium* (Kvastmossa)  
*Diplophyllum* sp. (Levermossa)  
*Hylecomnium splendens* (Husmossa)  
*Kiaera glacialis*  
*Kiaera starkei*  
*Lophozia* sp. (Flikmossor)  
*Pleurozium schreberi* (Väggmossa)  
*Pohlia nutans* (Nickmossa)  
*Polytrichum alpinum* (Nordlig björnmossa)  
*Polytrichum commune* (Björnmossa)  
*Polytrichum hyperboreum* (Hedbjörnmossa)  
*Polytrichum juniperinum* (Enbjörnmossa)  
*Polytrichum piliferum* (Hårbjörnmossa)  
*Polytrichum sexangulare*  
*Ptilidium ciliare* (Franslevermossa)  
*Sanionia uncinata*  
*Sphagnum* sp. (Vitmossa)

#### EVERGREEN PLANTS

*Andromeda polifolia* (Rosling)  
*Cassiope hypnoides* (Mossljung)  
*Diphasiastrum alpinum* (Fjälllumner)  
*Empetrum nigrum* (Kråkbär)  
*Phyllodoce caerulea* (Lappljung)  
*Vaccinium vitis-idaea* (Lingon)

#### HERBS

*Bistorta vivipara* (Ormrot)  
*Carex* sp. (Starrer)



Carex bigelowii (Vanlig styvstarr)  
Carex brunnescens (Nickstarr)  
Carex lachenalii (Ripstarr)  
Carex lapponica (Nordstarr)  
Carex rotundata (Rundstarr)  
Carex stenolepis (Gölstarr)  
Carex vaginata (Slidstarr)  
Cornus suecica (Hönsbär)  
Gnaphalium supinum (Fjällnoppa)  
Hieracium sect. alpina (Fjällfibbla)  
Hieracium sp. (Fibbla)  
Huperzia selago (Grodlummer)  
Juncus filiformis (Trådtåg)  
Juncus trifidus (Klynnetåg)  
Luzula multiflora (Ängsfryle)  
Luzula sp. (Frylen)  
Luzula spicata (Axfryle)  
Pedicularis lapponica (Lappspira)  
Pyrola minor (Klotptrola)  
Rubus chamaemorus (Hjortron)  
Rumex ssp. lapponicus (Lappsyra)  
Sibbaldia procumbens (Dvärgfingerört)  
Solidago virgaurea (Gullris)  
Trientalis europaea (Skogsstjärna)  
Viola biflora (Fjällviol)

#### LICHENS

Alectoria nigricans (Upprätt taggellav) ?  
Cetraria delisei (Flikig islandslav)  
Cetraria ericetorum (Smal islandslav)  
Cetraria islandica (Islandslav)  
Cladina mitis (Gulvit renlav)  
Cladina rangiferina (Grå renlav)  
Cladonia amaurocraea (Stor pigglav)  
Cladonia bellidiflora (Blombägarlav)  
Cladonia coccifera (Kochenillav)  
Cladonia crispata (Taggig bägarlav)  
Cladonia ecmocyna (Snöbägarlav)  
Cladonia furcata (Rislav)  
Cladonia gracilis (Stängellav)  
Cladonia macrophylla (Fjällig bägarlav)  
Cladonia pleurota (Mjölik kochenillav)  
Cladonia sp. (Bägarlavar)  
Cladonia subfurcata (Mossebägarlav)  
Cladonia sulphurina (Trasig pöslav)  
Cladonia uncialis (Pigglav)  
Nephroma arcticum (Norrlandslav)  
Ochrolechia sp. (Örnlavar)  
Peltigera leucophlebia (Ådrig torsklav)  
Peltigera rufescens (Krusig filtlav)

Stereocaulon sp. (Påskrislav)

DECIDUOUS PLANTS

Betula nana (Dvärgbjörk)

Salix herbacea (Dvärgvide)

Vaccinium myrtillus (Blåbär)

Vaccinium uliginosum (Odon)

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