Effects of moose density and supplementary feeding on field layer vegetation

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Abstract

Large mammalian herbivores have the potential to directly and indirectly affect the ecosystem they live in, such as plant structure and dynamics of vascular plants. The present study experimentally estimated the impact of moose density and moose feeding stations on field layer vegetation. The effects of browsing on the field layer vegetation from moose feeding stations are somewhat unanswered, and there are few studies referring to this problem. Supplementary feeding of moose in winter will lead to concentration of direct and indirect effects of moose around feeding stations. Grazing and trampling are direct impacts of herbivores on vegetation, whereas indirect effects by moose include changed light interception from tree layers, higher decomposition rates and changed nutrient cycling and distribution. In this study, only indirect effects are investigated. Landowners have supplied moose with ensilage bales, and the moose is only subsequently feed with silage in winter. Percentage of tree seedlings, shrubs and vascular plant species were registered at different distance from moose feeding stations. Six plots were placed in clusters at 25, 50, 100, 200, 500 and 1000 meters from the feeding station. Results show that moose feeding stations modified plant species composition and species richness along a gradient from the feeding station. A main effect of moose feeding station and moose density is a shift in field layer vegetation, where some species are more common at certain environmental conditions at different distances from feeding stations. This study highlights the effects of moose feeding stations on the environment in boreal forest, and will be relevant for landowners and wildlife biologist.

Key words: moose density, moose feeding stations, indirect effects, species richness, field layer vegetation, cluster analysis, plant composition.

Sammendrag

Store planteetende pattedyr som elgen (*Alces alces)* har evnen til å påvirke økosystemet de lever i, som strukturen og dynamikken til karplanter. Dette studiet har estimert innflytelsen av elgtetthet og fôringsstasjoner til elg på feltvegetasjonen i boreal skog. Små trær, lyng og urter i feltsjiktet ble estimert prosentvis og registrert, på ulik avstand fra foringsstasjonene. Effektene av beiting på feltvegetasjonen rundt foringsstasjoner er fremdeles ikke fullstendig kartlagt, og det er få studier som refererer til denne problemstillingen. Fôring av elg på vinteren vil føre til direkte og indirekte effekter av elg rundt fôringsstasjonene. Beiting og tråkking er de viktigste direkte påvirkningene store gressetere har på økosystemet de lever i, men i dette studiet er kun indirekte effekter undersøkt. Indirekte effekter fra elg på vegetasjonen, inkluderer blant annet forandret lysavskjæring fra trær, høyere nedbrytnings effekt, forandret næringssirkulasjon og fordeling av næring i jorda. Grunneiere har fôret elg med silo kontinuerlig på vinteren. Seks kvadratiske firkanter i grupper ble plassert i feltsjiktet på avstand 25, 50, 100, 200, 500 og 1000 meter fra fôringsstasjonene. Resultatene viser at fôringsstasjonene endret plantekomposisjonen og artsrikdommen langs en gradient fra fôringsstasjonene. Effektene av elgtettheten og fôringsstasjonene, er en forandring i feltvegetasjonen, hvor noen arter er mer vanlig enn andre ved ulike miljømessige påvirkninger langs gradienten, og ved ulik avstand til fôringsstasjonene. Dette studiet viser og fremhever effektene av fôringsstasjoner til elg på det lokale økosystemet i den boreale skogen, og vil være relevant for blant andre grunneiere og biologer innen flora- og fauna.

Nøkkel ord: elgtetthet, foringsstasjoner til elg, indirekte effekter, artsrikhet, feltvegetasjon, cluster analyse, plante komposisjon.

Introduction

Large mammalian herbivores have the potential to directly and indirectly affect the ecosystem they live in (Pastor et al 2003), such as plant structure and communities of plants and animals, as well as soil and other ecosystems (Pastor et al 2003, Persson 2005, Augustine 1998). Moose (*Alces alces)* may have positive and negative effects on their environment, and the effects of large herbivores on boreal forests are long lasting (Buhtz 2006). Moose is the largest member of the deer family and the largest herbivore in boreal forests. Large mammalian herbivores in boreal regions are all ruminants belonging to the order Artiodactyla, of which the signature species is the circumpolar moose (Pastor et al 2006). An adult moose consumes 3000-5000 kg of dry matter pr year (Pastor et al 1993 and 2003). Moose has an important role in the ecosystem, and might be considered as an ecosystem engineer; diminishing the ecosystem and the environment by browsing, trampling and deposition of urine and faeces (Pastor et al 1993 and 2003, Hester et al 2006).

Grazing and trampling are probably the most important direct impacts of herbivores and they affect all stages of plant development, from germination to seed production. Indirect effects by moose on vegetation include changed light interception from tree layers, changes in soil temperature and moisture, changes in microclimate, higher decomposition rates and changed nutrient cycling and distribution (Hester et al

2006). How herbivores affect nutrient cycles in boreal forests are important, and large mammalian herbivores enhance local soil nutrient availability, when they gather food over a wide area and concentrate it in small spots of dung, urine and carcasses (moose) (Pastor et al 2006:10). One moose may produce 15-20 fecal dung's pr day (Ingebretsen et al 1997), and droppings of faeces and urine change the nitrogen (N) and carbon (C) concentration in ecosystems (Pastor et al 1993). There are few data on how fluctuations in moose population density affect nitrogen cycling (Pastor et al 2006:10), but it has been suggested that nutrients will spread with moose faeces along a gradient, more or less concentric from the spot, and the concentrations in the surroundings are likely to increase over time (Pastor et al 1993). Therefore, an increase or a decrease in N abundance may alter plant species composition (Singer et al 2003). Mammalian herbivores may also forage selectively on the most nutritious plant parts and plant species. This exerts a long-term and wide spread selection pressure on the plant community (Pastor et al 2006:10) and reduces the amount of plant litter returned to the soil, which in turn also will change nutrient cycling and plant composition (Persson 2005).

The timing of domestic herbivore grazing/browsing can also be manipulated through management to avoid or reduce pressure on specific plant communities at certain times of the year (Hester et al 2002 and 2006), and it may also lead the moose away from highly trafficated roads and avoid traffic accidents (Gundersen et al 2004). Supplementary feeding of moose in winter, changes moose migration patterns and leads to concentration of direct and indirect effects of moose around feeding stations. Experimental studies have shown that mammalian behaviour may be altered by supplementary feeding (Gundersen et al 2004). Ungulates reduce their home range when they are fed, as shown in a study performed by Guillet, Bergstrøm and Cederlund (1996) in studies of roe deer (*Careolus careolus),* and Smith (1993) in studies of alpine red deer (*Cervus elaphus hippelaphus*). They might also move their core area closer to bait (white-tailed deer; Kilpatrick and Stober 2002). Wood and Wolfe (1988) showed in their study that feeding of the animals reduced the number of mule deer (*Odocoileus hemionus*) collisions along highways in Utah, USA. If the response to supplementary feeding is the same for other ungulates, for example moose, this is a clever way of altering mammalian behaviour (Gundersen et al 2004). Landowners in south east Norway has supplied moose with silage bales up to nineteen winters. The moose is only subsequently feed with silage in winter. The first moose feeding station was established during winter of 1989/1990 (Personal communication: Karen Marie Mathisen, Hedmark University College). It is reasonable to consider that it took some time before the moose learned to eat from the feeding stations and felt safe around it. The incentive with the feeding station has been to limit migratory movements into heavily trafficated areas and away from young forest plantations (Gundersen et al 2004). Supplementary feeding stations represent in some areas extremely high winter densities of moose, including high browsing pressure and high concentrations of moose dung and urine, containing digested silage. Gundersen (2004) found that there are a association between the amount of faeces and distance to feeding station, and it shows that the general moose activity is concentrated around feeding station, either because some moose spend more time close to the feeding stations, or because more moose aggregate around feeding stations. At feeding stations with high consumption of bales, browsing was generally low at distances more than 1000 meters from feeding station (Gundersen et al 2004). Browsing activity in the vegetation may reflect the fact that moose need other food items in addition to the supply of silage, and therefore will use other food while browsing near the feeding station. Within a local scale, the proportion of pine twigs browsed by moose decreased with increasing distance to the feeding station, and a higher proportion of pine twigs were browsed at intensely used feeding stations (Gundersen et al 2004). Moreover, other aspects of supplementary feeding, both positive and negative have emerged, in particular the spatial distribution of browsing activity and forest damage around feeding stations (Gundersen et al 2004). If the vegetation around the feeding stations is heavily browsed, this may be a negative effect on the ecosystem around the feeding stations, and if the feeding stations infact reduce traffic accidents among moose and motor vehicles, this may be a positive effect. However, there is not much knowledge about the negative or positive effects of the feeding stations, and there are not many studies done about the effects (Pastor et al 2003).

The distribution of moose around supplementary feeding stations makes it possible to study a gradient of effects of moose on the ecosystem, although some effects may be confounded by the co-variation between input of nutrients into the system from supplementary feeding and the effects of moose. Artificial feeding of moose implies a substantial addition of resources to the existing ecosystem. A proportion of these resources will be distributed in a roughly concentric pattern around the feeding station via moose dung and urine, containing digested silage. Field layer vegetation may be affected by changes in nutrient availability from moose dung and urine, in addition to other indirect effects from moose density and moose feeding stations, like changed microclimate, changed moisture and temperature, light interception and higher decomposition rates. All these indirect effects all function at the same time. Increased nutrient availability may lead to a relative increase in fast growing, deciduous field layer species like *Vaccinium myrtillus* and herbs, while decreased nutrient availability may enhance slow growing evergreen species such as *Vaccinium vitis-idaea* and *Empetrum nigrum*. We might therefore se a connection between plant responses to indirect effects from moose density and feeding stations, and distance to feeding station. The additional input of nutrient from faeces and urine from moose, containing silage, has not been much described or investigated earlier. In all other systems described by Pastor (1993, 2003, 2006) and others, nutrient that cycle through the moose, already exist in the nutrient system. The effects of browsing on the field layer vegetation from moose feeding stations are also somewhat unanswered, and there are few studies referring to this problem (Pastor et al 2003, Persson 2005).
The question to be investigated in this thesis is:
How are species richness and composition on the field layer vegetation affected by indirect effects from moose density and moose feeding stations?

Material and Methods

Study area

Study sites (figure 1) are situated in the middle boreal forest zone in middle of Norway, 230 kilometers north-east of Oslo, in Hedmark county and Stor-Elvdal municipality. The highest point in the municipality is 1767 meters above sea level (Brænd 1997). The study area is within the following coordinates: North- 32V0610496/6834752, South- 32V059839/681566, West- 32V0603415/6814379, and East- 32V0604473/6834797.

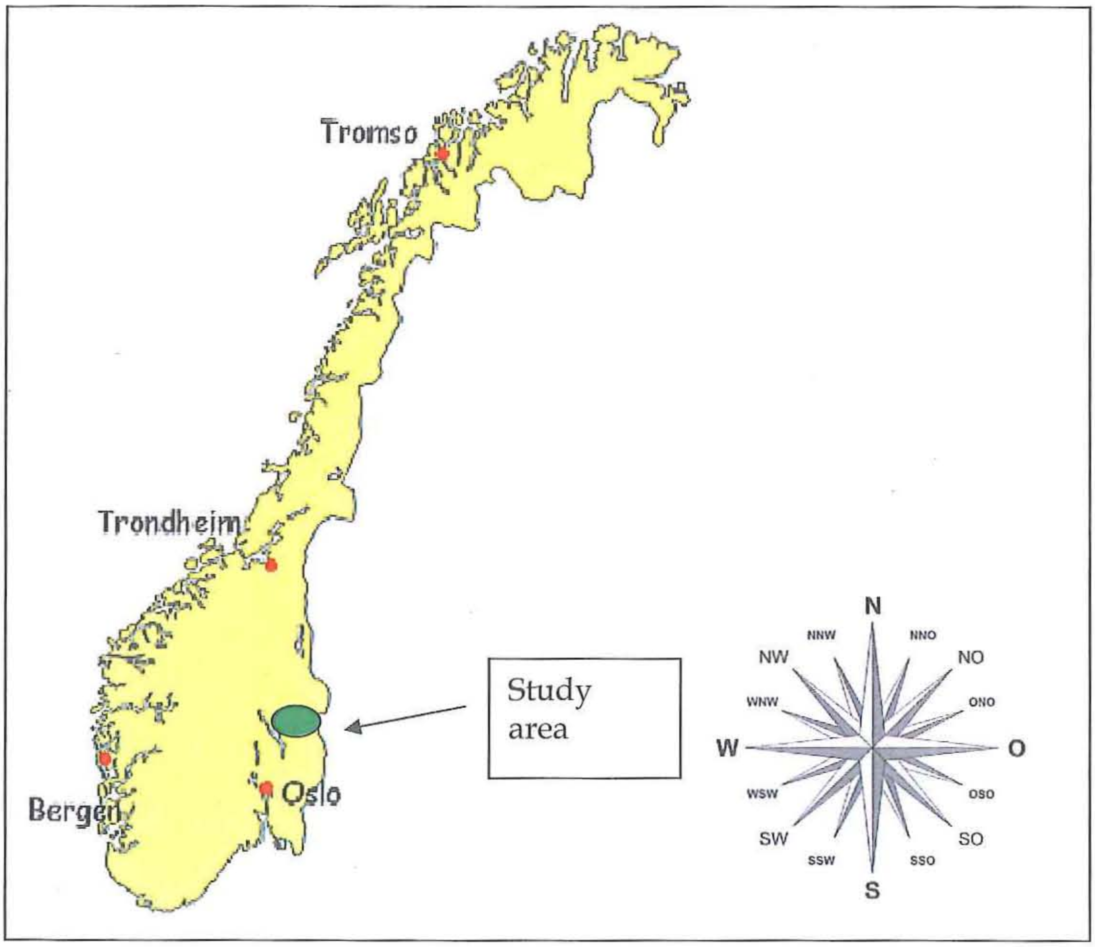

Figure 1: Map of Norway with marked study area.

Climate

The climate in Norway is affected by the north-Atlantic current. The middle boreal forest zone is characterized by short summers and long winters (Moen 1998), and moderate amount of precipitation (Brænd 1997). The topography varies in the study area and this leads to variation of precipitation in the study area and municipality. The northern area in Stor-Elvdal has more rainfall than the southern part (Brænd 1997). The temperature are higher down in the valleys, and decreases west in the municipality, decreasing with the increasing height above sea level (Brænd 1997). The area is covered with snow approximately 8 months pr year, starting in October and ending in May (Lystad 1978). From 1971-2000 maximum snow depth in Stor-Elvdal municipality was 250-500 mm (Se Norge. November 19 th, 2007: www.senorge.no). In Stor- Elvdal municipality the average temperature pr year is 6,4° C, with a total precipitation of 735 mm pr year in 2006 (Weather Climat. November 16 th, 2007: www.weatherclimat.com), and most of the rainfall occurs in summer (Brænd 1997).

The plants possibility to grow and reproduce in this area is highly dependent on temperature, and the whole growing season in the study area lasts from 140 until 160 days (Moen 1998, Brænd 1997). Growing season is defined by an average day temperature higher than >5°C (Moen 1998). This value is chosen as the average value of temperature because most plants have minimum growth in temperature lower than 5°C (Moen 1998). In Stor-Elvdal the growth period for the plants starts about 5.May and ends 28. September (Lystad 1978).

Geological substrate

The different rock type quality is important to the plant diversity and different vegetation types, which differs between regional and local areas. The bedrock type in the Stor-Elvdal municipality is mainly sparagmite and sandstone. In some areas in the municipality the bedrock is partly shale, and in other areas more rich minerals are found (Brænd 1997). Shale bedrock is not very nutritious for plant growth (Moen 1998, Brænd 1997). The large amount of glacier sediments connected to the areas around the river Glomma which runs through the whole municipality of Stor-Elvdal, is prominent. The rest of the municipality, the bedrock is covered with moraine soil of variable thicknesses (Brænd 1997).

Soil

The soil is affected by climate, vegetation and plant species diversity. The formation of the soil is dependent of the type of bedrock and the characteristic of the material above it. The inland ice from the early ice ages formed the morainsoil, which is covering the ground rock and covering most of the middle boreal forest zone and Stor-Elvdal municipality. The morainsoil holds fine and coarse particles, like for example clay. Deep moraine soil gives good growth conditions (Moen 1998). The deep moraine soil is used for food production. Peat soil is covering the moraine soil, and the moraine soil is covering the river sand, which found in the bottom of the valley by the river Glomma (Brænd 1997). The podsol, which is a profile, is covering the moraine soil (Caplex. January 16th, 2008: www.caplex.no).

Vegetation

Trough the northern part of Europe and Asia a mighty conifer tree belt covers parts of the land, including large parts of Hedmark County and Stor-Elvdal municipality. This Scandinavian forest belt is distinctive by its low number of plant species (Gjærevoll 1978) and is also a part of the circumpolar taiga. In Stor-Elvdal *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce) are the dominating species. Where the soil is moist, clean stands of *Picea abies* can be found. A mixed forest of these two species are most common, but there are also forests of deciduous trees, for example stands of *Betula Sp.* (Birch), growing up to 900 meters above sea level (Brænd 1997). *Pinus sylvestris* are a rougher tree species than *Picea abies* and grows at a higher level above the sea, and further north in Stor-Elvdal, increasing with the increasing height above sea level (Dahl 1963, Gjærevoll 1978 and Brænd 1997). Lichen- and dwarf shrub and stands of pine tree forests are found on dry and nutrient poor soil in the northern part of the municipality. The south-western part of Stor-Elvdal is dominated by mire. This vegetation type is usually species poor, and there are few species-rich swamps in the study area (Brænd 1997). The dominating species in the field layer vegetation are *Calluna vulgaris* (heather), *Vaccinium myrtillus* (blueberry) and *Vaccinium vitis-idaea* (lingonberry shrub) and *Empetrum nigrum* (crowberry shrub) with different grasses and herbs. If the has a good quality class, ferns are also present (Gjærevoll 1978).

Supplementary feeding of moose

Landowners in south east Norway has supplied winter feeding moose with ensilage bales since 1989, also called feeding stations. These locations are usually close to forest roads. The incentive with the feeding stations has been to limit migratory movements into heavily trafficated winter areas and away from young forest plantations (Gundersen et al 2004). There is about 5, 7 moose pr km^2 at 1000 meters from feeding station, using Stor-Elvdal municipality as their home range (Personal communication: Karen Marie Mathisen, Hedmark University College). In 2007, approximately 752 moose were shot during hunting in Stor-Elvdal municipality. Every year about 700 calves are born, and the yearly calf production is about 30% of the total number of moose density in the municipality (Personal communication: Håvard Haug, Stor-Elvdal municipality). In Stor- Elvdal the oldest feeding station is 19 years old (Personal communication: Karen Marie Mathisen, Hedmark University College), and there are about 50 feeding stations in the study areas Imsdalen- and Koppang in Stor-Elvdal municipality. Number of silage bales on each feeding station varies between 12 bales and 70 bales pr year (Personal communication: Stor-Elvdal Grunneier Forening). One feeding bale contains approximately 400-600 kilo of ensiled grass.

Data collection

In this paper I investigate the following question; *How are species richness and composition on the field layer vegetation affected by indirect effects from moose density and moose feeding stations?* To investigate this question, the following sampling methods were used; Percentage of cover of tree seedlings, shrubs and vascular plant species were registered in clusters of plots, at different distance from feeding station of moose. Six plots (1x1 m) were placed in clusters of six, at 25, 50, 100, 200, 500 and 1000 meters from the feeding station (figure 2) along a browsing gradient (transect). Plots were 4 meters apart in every direction (figure 2).

The field work was carried out during summer 2007. Field work period was from 20.07.07- 02.08.07, where I registered % of field layer vegetation cover.

The feeding stations and transects of sampling were chosen by age and number of silage bales on feeding station, where the old feeding stations were preferred, mainly because of the possible long-term effect from the feeding station on the environment. Feeding stations and transects for sampling used in this study were identified from maps and selected to have as similar environment (vegetation) as possible, and therefore avoiding strong altitudinal differences, vicinity of other feeding stations and immediate contact with roads and other constructions. There are 8 different feeding stations/transects in this investigation, located in different areas in Stor-Elvdal, Hedmark County. Transects were given the same name as the feeding stations, and were placed in the terrenge by using maps (maps nr: 1917 IV and 1918 III), and drawing a straight line with a liner and pencil on the maps. The line followed the height curves on the map, as accurate as possible.

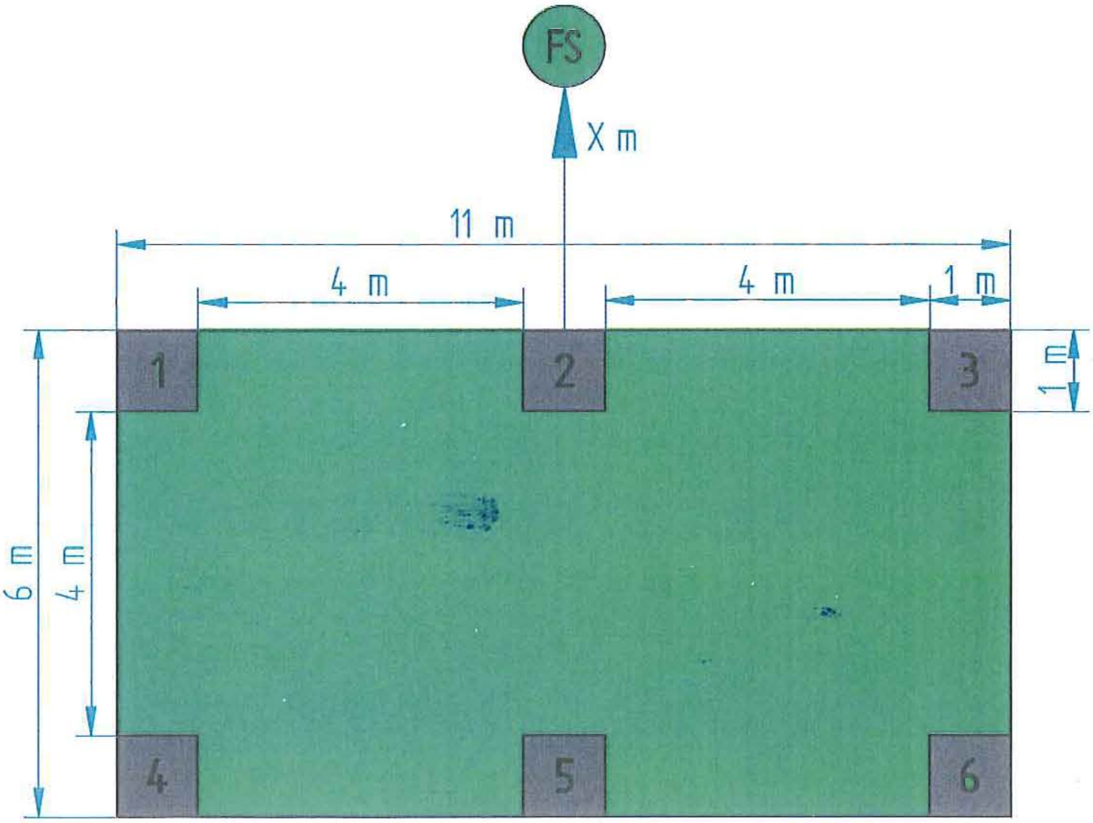

Figure 2: Cluster with plots (grey squares), and where FS are feeding station.

The transects were walked through before sampling started, using maps of the area locating the feeding stations, compass and gps, and at the same time making sure the clusters are not in a inappropriate location. There are several criteria that had to be fulfilled before the plots and clusters could be placed at the originally planned location. Both plots and clusters at locations had to have minimum 20% of one or several of the dwarf shrubs inside them (*Calluna vulgaris, Empetrum nigrum, Vaccinium vitis-idaea or Vaccinium myrtillus*). The clusters were placed at locations that not include clear cuts, bogs, and old farms, and had to be at least 20 meters from forest roads. The plots were placed at their originally planned location (1-6), unless they ended up in inorganic locations like large stones or roads. When moving a plot, it was moved 1 meter (figure 3), from start until the criteria were fulfilled. The cluster were also moved if the location were unsuitable, simply by moving it 20 meters right or left from the original location, facing the feeding station and having the same distance to feeding station. The procedure was to move it right first, then left. If 20 meters in right or left direction was not suitable; the cluster was moved 40 meters, than 60 meters and so on.

21	22	23	24	9
20	8	3	5	10
19	2	start	1	11
18	7	4	6	12
17	16	15	14	13

Figure 3: Direction and order when moving plots.

Transects and clusters were also identified using GPS (GPSMAP 60Cx) during fieldwork. This location in the cluster, defined by GPS and defining the distance from the feeding station, was the middle point in every cluster. The compass was used to point out the correct direction of the transect from feeding station. The plots were marked with wooden sticks, and each stick in each corner of the plots were marked with red tape to better view the plots in the shrub layer. The plots were lined up and square made by roap and key rings. There were totally 36 different plots in each transect, and a total of 288 sampling plots. Inside each sampling plot of 1 m^2 the cover percent of each species was registered. Cover was visually estimated in percentage for each species in the plot at the peak of the growing season in mid-July (table 1). Tree seedlings up to 50 cm high were also registered and % cover was visually estimated. For the statistical analysis I used the cover percent per species. The estimates of cover resulted in 1769 percent plant cover samples. All the information (counts and measurement) gathered at the feeding stations/gradient where written down in a form, using a new form at every feeding station.

Table 1: Table of species registered and cover estimated in the field

Species	**Reg. cover %**
Andromeda polifolia (Hvitlyng)	x
Bryophytes (Moser)	x
Calluna vulgaris (Røsslyng)	x
Deschampsia flexuosa (Smyle)	x
Empetrum nigrum (Krekling)	x
Epilobium angustifolium (Geitrams)	x
Equisetum sylvaticum (Skogsnelle)	x
Filipendula ulmaria (Mjødurt)	x
Fragaria vesca (Markjordbær)	x
Fungus (Sopp)	x
Galeopsis tetrahit (Hvassdå)	x
Geranium sylvaticum (Skogstorkenebb)	x
Graminids (Gress familien)	x
Gymnocarpium dryopteris (Fugletelg)	x
Juncaceae (Sivfamilien)	x
Lichens (Lav)	x
Linnaea borealis (Linnea)	x
Luzula Pilosa (Hårfrytle)	x
Lycopodium spp(Kråkefotfamilien)	x
Maianthemum bifolium (Maiblom)	x
Melampyrum spp (Marimjelle)	x
Melampyrum pratense (Stormarimjelle)	x
Melampyrum sylvaticum (Småmarimjelle)	x
Oxalis acetosella (Gjøkesyre)	x
Phegopteris connectilis (Hengevinge)	x
Picea abies (Gran)	x
Pinus sylvestris (Furu)	x
Rubus chamaemorus (Molte)	x
Rubus saxatilis (Tågebær)	x
Solidago virgaurea (Gullris)	x
Sorbus aucuparia (Rogn)	x
Trientalis europaea (Skogstjerne)	x
Unknown species	x
Vaccinium microcarpum (Små tranebær)	x
Vaccinium myrtillus (Blåbær)	x
Vaccinium uliginosum (Blokkebær)	x
Vaccinium vitis-idaea (Tyttebær)	x

Statistical methods

Abundance and performance of species depends on its relations to its physical and biological environment. This is what determents the composition of plant communities. This can be described and analysed by multivariate statistics.

Canoco for Windows 4.5 software is a program package for analysing ecological data (ter Braak et al 2002), and was used in this study to analyse field layer vegetation cover %, using ordination (gradient analyses) methods. Ordinations are methods to find structure or patterns in data. This is done by reducing number of independent variation or dimensions in the dataset. Patterns in the dataset will appear in the ordination diagram, and can be interpreted (Lepš et al 2003). The significance level in the Monte Carlo Permutation test of environment variables was set to P< 0, 05, which means that there is less than 5% probability that the observed effect is a result of chance, and not a real effect (McKillup 2005). This is statistical tests of the relations between the response variable data and each of the explanatory variables. One statistical unit, or one sample, in this study is one cluster. To test if there is a significant difference in species richness between different distances from feeding station, I used 1-factor variance analysis, Anova models.

In this dataset species abundance are the responsvariables. Explanatory variables or environment variables in this study are study areas (Imsdalen and Koppang), mean number of ensilage bales on feeding station (mean fee), height above sea level (h.o.h) and distance to feeding station from cluster/plot (distance). Both response and explanatory variables were used in indirect (unconstrained) and direct (constrained) analyses. Unimodal methods were used because this method fitted the dataset better than a linear response method (Lepš et al 2003). Correspondence analysis (CA) and canonical correspondence analysis (CCA), with a unimodal response model, were used because species are expected to have unimodal response along the gradient or ordination axis. Detrended correspondence analysis (DCA) was also used. In the correspondence, detrended correspondence and canonical correspondence analyses I looked for how the species spread in the ordination diagram and how they are correlated by the explanatory variables. For the interpretation of CA, CCA and DCA diagrams, the biplot rule was used. Biplot is an ordination diagram displaying two different kinds of objects (species and samples, or samples and environment variables). Interpretation proceeds by projecting points on directions defined by arrows or gradients in the biplot. The length of the gradients indicates the importance of that gradient in the ordination diagram. The higher residuals the species have from the perpendicular line in the ordination diagram, the higher correlated the species are to the explanatory variable. Correlation index between the environment variables and the ordination axis are also used to interpret the ordination diagram. Eigen values of the ordination axis measures the importance of the ordination axis, expressed as the amount of variability in the primary data (response data), and are explained by the corresponding axis. Eigenvalues are used to interpret the ordination diagram. High eigenvalue indicate high importance of the ordination axis (Lepš et al. 2003).

The response variables and the explanatory variables were analyzed using feeding station and clusters 25-1000 meter from the feeding station. To investigate if distance to feeding station has an effect on the species and samples distribution along transects, correspondence analysis (CA) was run with response variable and explanatory variables. CA gives an ordination that is calculated from the species data only, and is used in this study to look at the species distribution along the gradient. It shows the major patterns in species data, irrespective of any explanatory variables. The explanatory variables may be added according to the best fit. A correspondence analysis presumes that the structure from the response variables, as result from a correspondence analysis, is independent of the explanatory variables. The diagram from the analysis describes a gradient but not the environment variables. However, to give an ecological interpretation of the ordination diagram from the analysis, these environmental variables must be understood. The ordination axis is theoretical gradients that best explain the species data. The axes are not constrained to be aggregates of the available variables (unconstrained ordination). The CA analysis was also modified to remove artificial arc shape. This include that the ordination axes are rescaled, and this analysis are called detrending (DCA). In detrending the relation between the first and the second axes causing the arc effect is removed by dividing the first axis in segments. Within each segment site scores are adjusted by reducing their values with their average value on the second axis, i.e., all scores are "moved" towards the first axis (Personal communication: Christina Skarpe, Hedmark University College). A canonical correspondence analysis (CCA) detects the portion of variation in the response data that is explained by the given explanatory data. Direct gradient analysis (CCA) gives an ordination with an optimal environmental basis. It show only those patterns in the species data that can be explained by the available environmental data, and it shows the amount of variation in species data which are best explained by given explanatory variables. The ordination axes are aggregates of the explanatory variables that best explain the species data. This is a form of regression analysis; species are explained by the environment via a small number of ordination axis (ter Braak et al 2002). Ordination diagrams have several ordination axes, and environment variables can be correlated to all of these. The ordination diagrams will only show two of these axes, and which axis the diagram is set to visualize can be chosen in Canoco. In this experiment, CCA ordination diagrams are visualised with first and second axis and second and third axis, depending on which axis the environment variable are correlated to.

The dataset were log transformed in Canoco for several purposes. To obtain statistically normal distribution of variables, and give less weight to dominant species, or give more weight to qualitative aspects of the data, log transformation can be useful (Lepš et al. 1995). Rare species were automatically down weighted in Canoco to reduce the effect of these species on the other species distribution in the ordination diagram (ter Braak et al. 2002). Covariables are explanatory variables, which are used as a "background" variable in an ordination diagram (Lepš et al. 2003). In this study, explanatory variables "height above sea level" (h.o.h), and study areas "Koppang"/"Imsdalen" are used as covariables. These variables are used as a "block factor" in experimental design, and are used to test explanatory variables. Their effect on the species in the diagram is not judged, as they are not visualized in it. Only the explanatory variables of which the effect we would like to interpret, are visualized (Lepš et al. 2003).

The species names in the ordination diagrams are shortened down to the first three letters and last four letters in the scientific name of the species.

Results

Environment variables "mean nr of silage bales on feeding station" and "distance to feeding station" accounted for most of the variation in the species data, using a detrended correspondence analysis (DCA) (figure 1). The figure show there is a grouping of some species around "mean nr of silage bales on feeding station" and "distance to feeding station". Environment variable "mean nr of silage bales on feeding station" is correlated to axes 1 (Correlation coefficient: 0.6572). This is also the variable which has the largest influence in the ordination diagram, visualized by the long arrow. Species like *Maianthemum bifolium, Geranium sylvaticum, Gymnocarpium dryopteris, Equisetum sylvaticum* and *Oxalis acetosella* are highly positively correlated to this variable, and indicate that these species are common at feeding stations with high number of silage bales and winter feeding moose. Species like *Vaccinium uliginosum, Andromeda polifolia, Calluna vulgaris* and *Vaccinium microcarpum* are highly negatively correlated to "mean nr of silage bales on feeding station", which indicate that these species are less common in areas with high number of silage bales and winter feeding moose. *Vaccinium uliginosum, Andromeda polifolia, Calluna vulgaris* and *Vaccinium microcarpum* are highly positive correlated to the environment variable "distance to feeding station"(figure 1), indicating that these species are common far from feeding station. There are several species highly negatively correlated to the variable "distance to feeding station", for example *Maianthemum bifolium, Geranium sylvaticum, Gymnocarpium dryopteris, Oxalis acetosella, Lycopodium spp, Oxalis acetosella* and *Equisetum sylvaticum* , indicating that they are common close to feeding station. "Distance to feeding station" is correlated to ordination axis 3 (Correlation coefficient: 0.0333). Environment variable "Koppang", which is also one of the study areas, are characterized by dwarf shrubs like *Vaccinium vitis-idaea, Calluna vulgaris, Empterum nigrum* and *Vaccinium uliginosum*, as well as forbs like Graminids, whereas environment variable and study area "Imsdalen" has dwarf shrubs like *Vaccinium myrtillus*, and forbs like *Deschampsia flexuosa Melampyrum spp, Maianthemum bifolium, Linnaea borealis, Geranium sylvaticum* and deciduous tree seedlings like *Betula spp* (birch) (figure 1). "Koppang" are correlated to ordination axis 2 (Correlation coefficient: 0.0698), whereas environment variable "Imsdalen" is correlated to ordination axis 1 (Correlation coefficient: 0.8047). Species like *Solidago virgaurea* and *Fragaria vesca* show the highest positive correlation with environment variable "height above sea level", indicating that they are more common in areas high above sea level (figure 1). Graminids, *Pinus sylvestris*, Lichens, *Vaccinium microcarpum, Calluna vulgaris, Empetrum nigrum* and *Bryophytes spp* are also positively correlated to "height above sea level". *Filipendula ulmaria, Phegopteris connectilis* and *Rubus saxatilis* show the most negative correlation to "height above sea level", indicating that they are less common in areas high above sea level. Species like *Gymnocarpium dryopteris, Lycopodium spp, Oxalis acetosella* and *Equisetum sylvaticum* are also negatively correlated with "height above sea level", and the variable is correlated to axes 2 (Correlation coefficient: 0.1748). Species like *Maianthemum bifolium, Geranium sylvaticum, Gymnocarpium dryopteris, Equisetum sylvaticum, Oxalis acetosella* and *Fragaria vesca* are highly positively correlated to the environment variable "age of feeding station"(figure 1), and indicating that these species are common at old feeding stations. Environment variable "age of feeding station" is correlated to ordination axis 1 (Correlation coefficient: 0.2335). Species like *Vaccinium uliginosum, Andromeda polifolia, Calluna vulgaris* and *Vaccinium microcarpum* are highly negatively correlated to "age of feeding station", and suggest that these species are less common at older feeding stations.

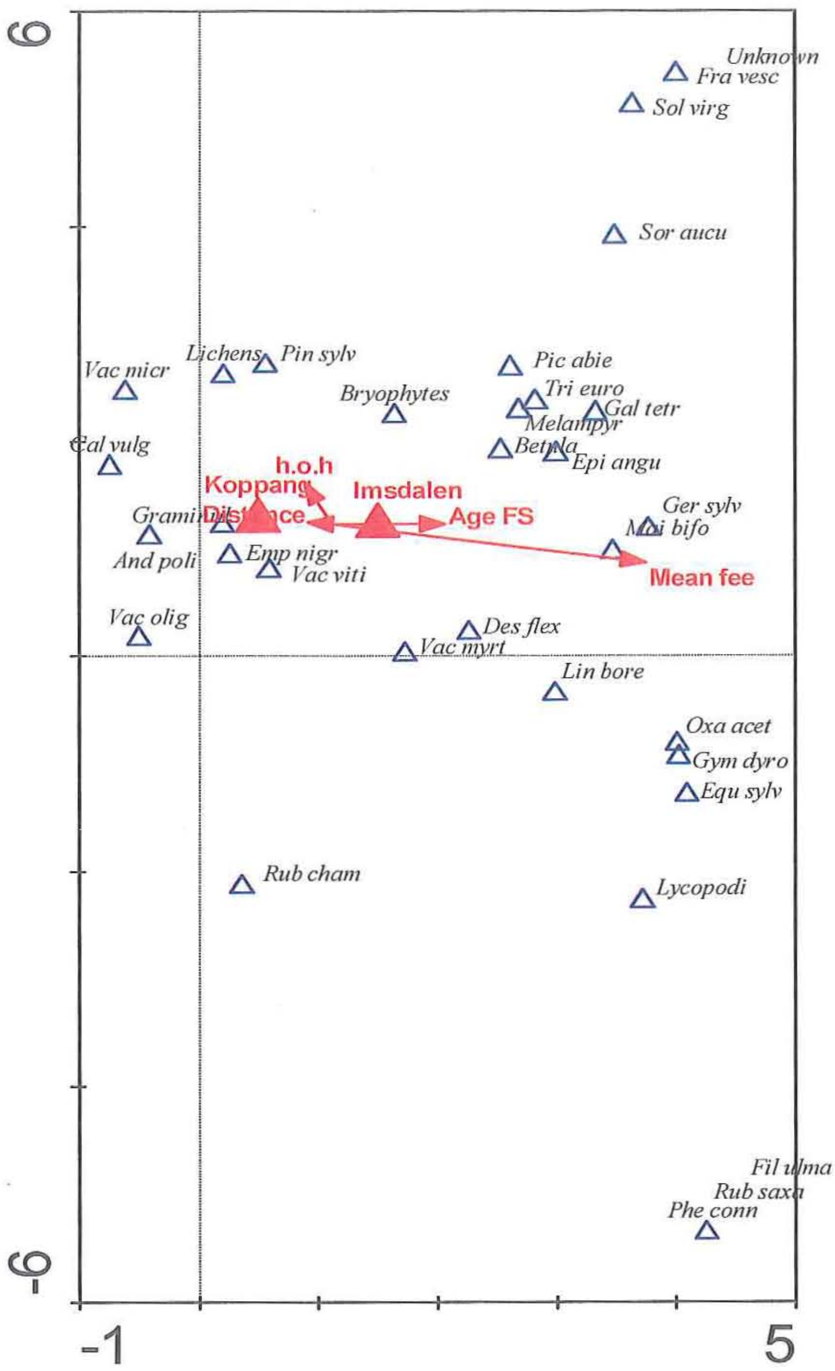

Figure 1: DCA analysis with axes 1 and 2, 25-1000meters. Rare species are down-weighted automatically in Canoco. The dataset are also log- transformed in Canoco. Environment variables "Age FS", "distance" and "h.o.h" visualized as arrows. Environment variables Imsdalen and Koppang are study areas in the experiment, and visualized as points. Environment variable are: "mean fee"- mean nr of silage bales on feeding station, "Age FS"- age of feeding station and "distance"- distance from feeding station and "h.o.h"- height above sea level.

Table 1: Summary of statistics in Canoco programme from a detrended correspondence analysis (DCA) ordination diagram in figure 1.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.326	0.091	0.042	0.028	1.121
Lengths of gradient	2.319	1.676	1.256	1.012	
Species-environment correlations :	0.842	0.517	0.245	0.449	
Cumulative percentage variance					
of species data :	29.0	37.2	40.9	43.4	
of species-environment relation:	53.0	58.8	0.0	0.0	
Sum of all eigenvalues					1.121
Sum of all canonical eigenvalues					0.423

Figure 2 shows species distribution affected by environment variables, along the gradient from a canonical correspondence analysis (CCA) with first and second ordination axis. *Betula spp* is highly positively correlated to the variable" age of feeding station" and " Distance to feeding station" in figure 2, indicating these specie are common at old feeding stations with high effect on the environment. *Empetrum nigrum, Pinus sylvestris, Bryophytes spp, Calluna vulgaris, Vaccinium vitis-idaea* and Lichens are also positively correlated to the variable" age of feeding station" and " distance to feeding station" in figure 2. " Age of feeding station" is correlated to ordination axis 2 (Correlation coefficient: 0.3417) (figure 2 and 3). *Empetrum nigrum, Pinus sylvestris* and Lichens are positively correlated to the variable" distance to feeding station" (figure 2), suggesting that these species are common far from feeding station. " Distance to feeding station" are correlated to ordination axis 3 (Correlation coefficient: 0.4336) (figure 3). Several of the same species positive correlated to "mean nr of silage bales on feeding station" are at the same time negative correlated to "distance to feeding station" and "age on feeding station" (figure 2), for example *Linnaea borealis, Oxalis acetosella, Gymnocarpium dryopteris, Lycopodium spp, Equisetum sylvaticum, Phegopteris connectilis, Rubus saxatilis, Filipendula ulmaria.* Where as *Geranium sylvaticum, Rubus chamaemorus, Fragaria vesca, Solidago virgaurea* and *Galeopsis tetrahit* are highly negative correlated to "distance to feeding station" and "age on feeding station" (figure 2), indicating that these species are common close to feeding station and less common at old feeding stations. Species like *Phegopteris connectilis, Rubus saxatilis, Filipendula ulmaria* are highly positive correlated to "mean nr of silage bales on feeding station" , whereas *Calluna vulgaris, Vaccinium vitis-idaea, Trientalis europaea, Deschampsia flexuosa, Epilobium angustifolium, Linnaea borealis, Oxalis acetosella, Gymnocarpium dryopteris, Lycopodium spp* are less positively correlated to environment variable "mean nr of silage bales on feeding station" in figure 2, indicating that these species are more common at sites with high winter feeding intensity and high number of silage bales. Environment variable "mean nr of silage bales on feeding station" are correlated to ordination axis 1 (Correlation coefficient: 0.8899) (figure 2 and 3). *Betula spp, Empetrum nigrum, Pinus sylvestris,* Lichens, *Melampyrum spp, Bryophytes spp, Vaccinium uliginosum, Picea abies, Sorbus aucuparia,* Graminids, *Fragaria vesca, Solidago virgaurea* and *Galeopsis tetrahit* negative correlated to environment variable "mean nr of silage bales on feeding station", where as *Andromeda polifolia* and *Vaccinium microcarpum* are highly negative correlated to environment variable "mean nr of silage bales on feeding station", indicating that these species are less common at feeding sites with high winter feeding intensity.

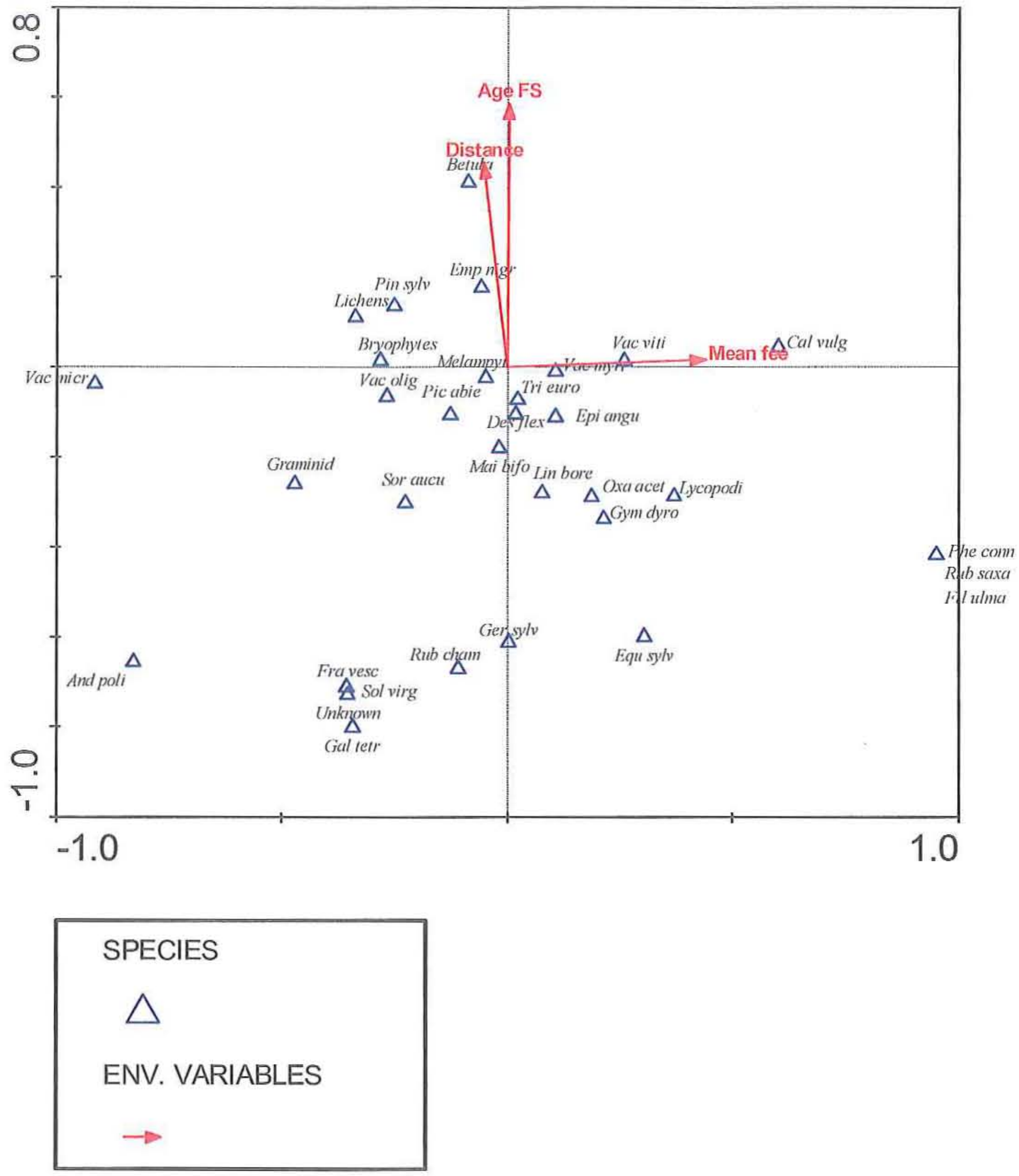

Figure 2: CCA analysis, with 1 and 2 axis, 25-1000m. Rare species are automatically down weighted in Canoco. The dataset are log transformed. The environment variables are selected manually, using forward selection. In the diagram, environment variables height above sea level and the study areas Imsdalen/Koppang are co-variables. Environment variable are: "mean fee"- mean nr of silage bales on feeding station, "Age FS"- age on feeding station and "distance"- distance from feeding station.

Table 2: Summary of canonical correspondence analysis from figure 2. Environment variables are manually selected, using forward selection. Significant environment variables are "mean nr of silage bales on feeding station". Environment variables are divided into two groups in the table; "before taken into the model", and "after taken into the model". Environment variables: "mean fee"- mean nr of silage bales on feeding station, "Age FS"- age on feeding station, "Distance"- Distance to feeding station.

	Before taken into the model	Variance explained by variables selected	**After taken into the model**	Variance explained by variables selected	Cumulative percentage variance explained of species data	Cumulative percentage variance explained of species-environment relation	Sum of all eigenvalues	Sum of all canonical eigenvalues
Mean fee	P-value: 0.0020 F-ratio: 5.537	0.143	P-value: 0.0020 F-ratio: 5.54	0.14	Axis 1: 16.7 Axis 2: 21.4 Axis 3: 23.6 Axis 4: 45.7	Axis 1: 70.9 Axis 2: 90.6 Axis 3: 100.0 Axis 4: 0.0		
Age FS	P-value: 0.2140 F-ratio: 1.365	0.040	P-value: 0.1160 F-ratio: 1.59	0.18				
Distance	P-value: 0.7320 F-ratio: 0.732	0.022	P-value: 0.6040 F-ratio: 0.84	0.20				
Total		0.205		0.52			0.867	0.205

Figure 3 shows species distribution affected by environment variables, along the gradient from a canonical correspondence analysis (CCA) with second and third ordination axis. Environment variable "distance to feeding station "is correlated to ordination axis 3 (Correlation coefficient: 0.4336) (figure 3), and has the most explanatory power in the diagram, visualized by the long arrow. *Vaccinium microcarpum* and *Andromeda polifolia* are highly positive correlated to "distance to feeding station" (figure 3). *Empetrum nigrum, Vaccinium vitis-idaea, Melampyrum spp, Bryophytes spp and Vaccinium myrtillus* are also positive correlated to "distance to feeding station". *Phegopteris connectilis, Rubus saxatilis, Filipendula ulmaria, Equisetum sylvaticum, Lycopodium spp, Fragaria vesca, Solidago virgaurea, Epilobium angustifolium* and *Galeopsis tetrahit* has the most negative correlation to "distance to feeding station".

Phegopteris connectilis, Rubus saxatilis and *Filipendula ulmaria* tend to cluster together in ordination diagrams (figure 1, 2 and 3), suggesting that they might have common environmental needs. *Oxalis acetosella* and *Gymnocarpium dryopteris* also tend to appear close together in the diagrams (figure 1, 2 and 3); again suggesting they might have similar environment demands for growing and reproducing, as well as *Pinus sylvestris* and Lichens. Sum of all eigenvalue or total intertia in figure 1 is high (1.121), compared to eigenvalue in figure 2 and 3 (table 2 and 3), and indicate that figure 1 explains the relationship between the species in the samples well (table 1), using a detrended correspondence analysis.

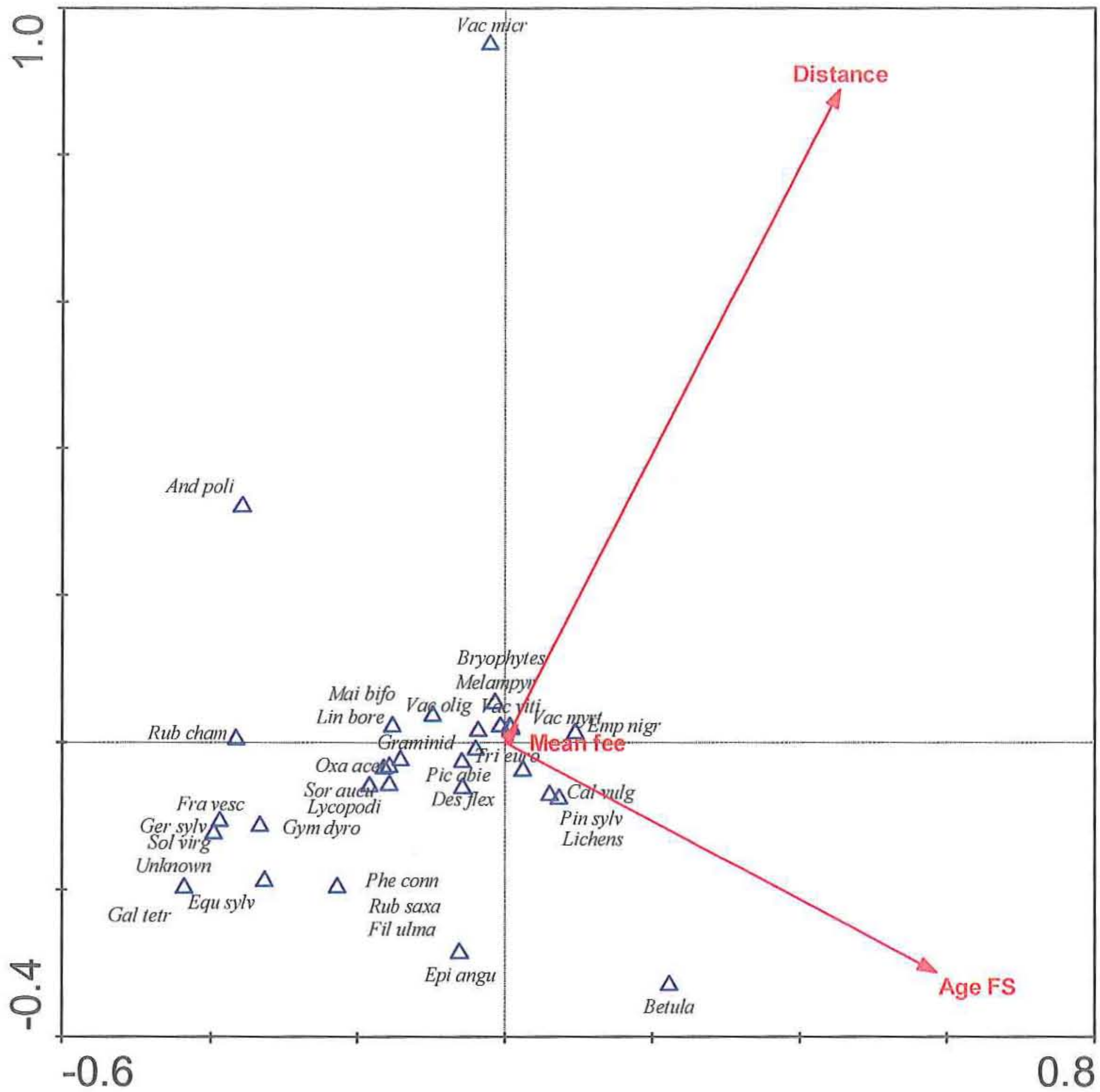

Figure 3: CCA analysis, with 2 and 3 axis, 25-1000m. Rare species are automatically down weighted in Canoco. The dataset are log transformed. The environment variables are selected manually, using forward selection. In the diagram, environment variables height above sea level and the study areas Imsdalen/Koppang are co-variables. Environment variable are: "mean fee"- mean nr of silage bales on feeding station, "Age FS"- age on feeding station and "distance"- distance from feeding station.

Table 3: Summary of canonical correspondence analysis from figure 3. Environment variables are manually selected, using forward selection. Significant environment variables are "mean nr of silage bales on feeding station". Environment variables are divided into two groups in the table; "before taken into the model", and "after taken into the model". Environment variables: "mean fee"- mean nr of silage bales on feeding station, "Age FS"- age on feeding station, "Distance"- Distance to feeding station.

	Before taken into the model	Variance explained by variables selected	**After taken into the model**	Variance explained by variables selected	Cumulative percentage variance explained of species data	Cumulative percentage variance explained of species-environment relation	Sum of all eigenvalues	Sum of all canonical eigenvalues
Mean fee	P-value: 0.0020 F-ratio: 7.209	0.119	P-value: 0.0020 F-ratio: 7.21	0.12	Axis 1: 14.1 Axis 2: 16.5 Axis 3: 17.4 Axis 4: 38.1	Axis 1: 81.1 Axis 2: 94.4 Axis 3: 100.0 Axis 4: 0.0		
Age FS	P-value: 0.5240 F-ratio: 0.910	0.017	P-value: 0.4140 F-ratio: 1.04	0.14				
Distance	P-value: 0.8780 F-ratio: 0.576	0.011	P-value: 0.7740 F-ratio: 0.68	0.15				
Total		0.147		0.147			0.846	0.147

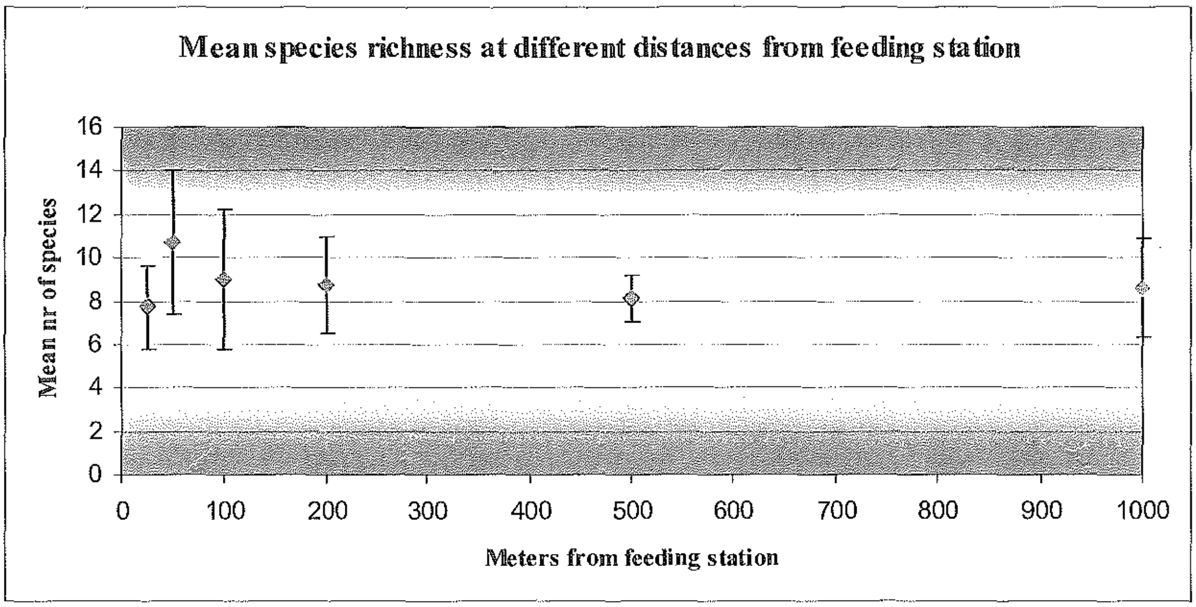

Figure 4: Diagram showing mean species richness at different distances from different feeding stations, and two times standard error.

There is no significant difference between species richness in any of the six distances from feeding station ($F_{5,42}$= 0, 72, p=0, 613).

Discussion

My experimental results show that field layer vegetation are indirectly affected by moose density and moose feeding stations, and I found plant composition and species richness to vary along the transects/gradients from feeding station. Moose browsing is intense at feeding stations and decreases with increasing distance to feeding station (Gundersen 2004). This study does not investigate the direct effects of moose density, but only indirect effects of moose density and moose feeding stations. Indirect effects caused by browsing in the tree canopy are reduced litterfall, which will decrease plant litter to the soil and therefore decrease nutrient input, and at the same time increase light interception (Persson 2005). Small tree canopies are browsed at feeding stations in addition to silage, but field layer vegetation is not browsed in winter when vegetation is covered with ice and snow. Moose dung has a low nutrient content and may decrease nutrient availability (Pastor 1993) but at feeding stations silage forage may affect moose dung to be more degradable, and release more nutrients. Indirect effects from moose feeding stations are not the only environmental conditions affecting plant species. Other important environment conditions, for example soil moisture, microclimate and elevation (Poulos 2007), might also affect growing conditions, but it is assumed these conditions have no connection to moose density, and they are therefore not further investigated. The three most important explanatory variables which I have analysed to investigate indirect effects are "mean nr of silage on feeding station", "age on feeding station" and "distance to feeding station". In this chapter, figure 2 in results is used to discuss how the explanatory variables affect the species composition. Further, common field layer species such as *Vaccinium myrtillus, Calluna vulgaris, Vaccinium vitis-idaea* and *Deschampsia flexuosa* are discussed.

My results show no significant difference in species richness between distances from feeding station. High abundance of moose will decrease soil nutrients by browsing on tree canopy (Persson 2005), because plant litter is the main source of soil nutrients, and especially of nitrogen (Persson 2005, Pastor 2003). An increase in soil nutrients by faeces and urine, and a decrease in nutrients by reduced plant litter close to feeding station, may increase or decrease % cover for several plant species. High moose browsing pressure is expected to have a negative effect on accessibility of nutrients for plant (Persson 2005). At 25 meters from feeding station, it is likely that the abundance of moose is extremely high, and plant species are damaged by trampling and the soil is covered with faeces. These conditions are not likely to give good growing conditions for plants. This will further not increase % cover or species richness; instead it will most likely decrease. At 50 meters from feeding station moose density are lower than at 25 meters, but still high, and further the distribution of moose faeces and urine are more distributed around feeding station, and better adapted for plant production, and resulting in increased species richness and vegetation cover. Species richness as well as nutrient richness (Pastor 2003) were assumed to decrease beyond 50 meters from feeding station because of intense browsing on tree canopy by moose, reducing plant litter to the ground, and therefore reducing nutrients to the soil, as well as reduced dropping of faeces and urine. High browsing pressure on tree canopy will also increase light to the ground, and this might also lead to changes in species composition, in addition to a shift in soil nutrients.

Results show that common species in boreal forest, like *Vaccinium myrtillus* might be indirectly affected by high density of winter feeding moose, indicated by the positive correlation to environment variable "mean nr of silage bales on feeding station". Feeding stations with a high number of bales have a high number of winter feeding moose distributed around it, and browsing pressure on trees around feeding station and deposition of faeces and urine with digested silage, is intense. The additional nutrient input from moose faeces and urine with digested silage may explain why *Vaccinium myrtillus* are common in areas with high density of winter feeding moose.

Vaccinium myrtillus has wintergreen stems and is adapted to survive the winter under snow cover (Buhtz 2006), and is usually not browsed by moose when covered with snow and ice. Further, my results show that *Vaccinium myrtillus* is common close to feeding stations, indicated by negative correlation to environment variable "distance to feeding station". *Vaccinium myrtillus* is more often found on nitrogen poor soil, than intermediate/nitrogen rich soil (Vevle 1982). *Vaccinium myrtillus* is less common at old feeding stations, which have a large effect on the environment, because of the long term effects. Indirect effects from feeding stations earlier mentioned might therefore be enhanced at old feeding stations, because of browsing in the tree canopy and dropping of faeces and urine over a longer time scale. It is possible that the increase in nutrients through dropping of urine and faeces are affecting cover % of *Vaccinium myrtillus* more than the negative effect of reduced shade due to high browsing pressure in tree canopy and reduced soil nutrients by browsing on tree canopy, and therefore found at high moose density. Buhtz (2006) found an indirect negative effect on flowering on *Vaccinium myrtillus,* when analysing simulated effects of moose density and habitat productivity due to high moose density, whilst this study shows indirect positive effects at high moose densities. Results also show that *Vaccinium vitis-idaea* was more common than *Vaccinium myrtillus* at feeding stations with high number of silage bales. This can be explained by changes in environmental conditions due to the high moose activity around feeding stations, such as changes in nutrient availability and changed light interception. The changes in nutrient conditions and light interception due to browsing are likely favourable for *Vaccinium vitis-idaea,* and therefore indirectly positive affected by moose feeding stations and moose density. Browsing in tree canopy, resulting in increased light interception due to high moose density around feeding stations, might have changed competition between *Vaccinium vitis-idaea* and *Vaccinium myrtillus,* which was also found by Buhtz (2006). Ordination diagram also show that *Vaccinium vitis-idaea* are found at old feeding stations with high and long-term effect on the environment, whereas *Vaccinium myrtillus* are less abundant at old feeding stations. The study performed by Buhtz (2006) also found that there is a correlation between *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, indicating they will affect each other in a species composition shift.

The positive correlation between *Calluna vulgaris* and "mean nr of silage bales on feeding station" indicate that *Calluna vulgaris* is more abundant in areas with high intensity of winter feeding moose. *Calluna vulgaris* preferres habitats which have sandy and nutrient poor soil (Britton 2003, Lid 2005). Britton (2003) showed in a experiment that addition of nitrogen in soil had little effect on species cover and shoot biomass of *Calluna vulgaris*, and on sandy soil *Calluna vulgaris* are able to regain dominance relatively quick after disturbance. This may explain why *Calluna vulgaris* are abundant at high winter feeding intensity. *Deschampsia flexuosa*, which is a nutrient demanding species (Britton 2003), is more abundant than *Calluna vulgaris* close to feeding station, showed by a negative correlation to "distance to feeding station". This can be explained by the high deposition of urine and faeces close to feeding station, and further increase nitrogen to the soil, and increased light interception due to browsing on tree canopy. Also, my results show that *Deschampsia flexuosa* is more common closer to feeding station than *Vaccinium myrtillus*, also indicated by the higher negative correlation to "distance to feeding station". *Deschampsia flexuosa* is also common at feeding stations with high intensity of winter feeding by moose, showed by the positive correlation to environment variable "mean nr of silage bales on feeding station". This can be explained by indirect effects from moose feeding stations, by increased nutrient input to the soil from faeces and urine, with digested silage. Buhtz (2006) suggest that nitrogen input from urine and faeces might shift the plant composition in favour of more nitrogen demanding plant species, like *Deschampsia flexuosa*. This theory is also supported by Britton (2003), where replacement of dwarf-shrubs by grasses has been linked to high levels of nitrogen deposition. Buhtz (2006) also found that *Vaccinium myrtillus* and *Deschampsia flexuosa* might be correlated to each other, indicating that these two species might affect each other in a species composition shift, due to nutrient change and light interception.

Summary observations

My results show no significant difference in species richness between distances from feeding station. *Vaccinium myrtillus* are positive correlated to environment variable "mean nr of silage bales on feeding station", and therefore found at feeding stations with high number of silage bales and high intensity of winterfeeding moose. *Vaccinium myrtillus* is also common close to feeding stations, indicated by negative correlation to environment variable "distance to feeding station". *Vaccinium myrtillus* is also less abundant at old feeding stations, which have a large effect on the environment, possible because of the long term effects. *Vaccinium vitis-idaea* is more common in areas with high density of winter feeding moose than *Vaccinium myrtillus,* shown by the higher positive correlation with "mean nr of silage bales on feeding station", and also found at old feeding stations, shown by the positive correlation to "distance to feeding station". The positive correlation between *Calluna vulgaris* and "mean nr of silage bales on feeding station" indicate that *Calluna vulgaris* is more abundant in areas with high intensity of winter feeding moose. *Deschampsia flexuosa* is also common at feeding stations with high intensity of winter feeding by moose, showed by the positive correlation to environment variable "mean nr of silage bales on feeding station", but still less positive correlated than *Calluna vulgaris.* Indirect positive effects have been observed for all shrub species discussed in this chapter; *Vaccinium myrtillus, Calluna vulgaris, Vaccinium vitis-idaea* and *Deschampsia flexuosa.*

Additional nutrient input through moose faeces and urine with digested silage seems to be the indirect effect from moose density and moose feeding stations which has the largest influence on species composition and species richness around moose feeding stations.

Also, one of the main conclusions in my study is that moose density and moose feeding stations has an impact on plant species composition and richness along a gradient from feeding station. Through this effect, the impact of moose density over time, has the potential to change environmental conditions of vascular plant species in the field layer vegetation of the boreal forest. Moreover, ecosystems are also affected by moose density and feeding stations and it is important to investigate these effects further for future ungulate species, habitats, ecosystems and property management.

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I dedicate this master thesis to my father, Morten Olav Torgersen, who has given irrepressible support and encouragement through all my education, and work with this master thesis. Thank you.

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