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THE EFFECTS OF EXCLUSION OF BROWSING MOOSE ON ABOVE GROUND CARBON STOCKS IN EARLY SUCCESSIONAL STAGES IN BOREAL FORESTS

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ABSTRACT

Climate change can occur due to the rising of CO_2 in the atmosphere. Understanding factors that can increase atmospheric CO_2 is very important to decrease global temperature. There are many publications that investigate the effect of climate change and deforestation on above ground C stock. However few researches done on other factors that can change the amount of C stock. This study investigates the effect of moose browsing on above ground C stock in sucssetional boreal forests.

Boreal forests are a habitat for different animals and plants. Studying the relationship of herbivory and plants used to investigate their interaction effect on ecosystem. The objective of this study is to investigate the impact of moose browsing on above ground biomass and C stock in boreal ecosystem. In this study data were collected from 15 browsed and unbrowsed recent clear-cut treatments in Norwegian boreal forests.

The result indicated that even though, the deciduous species showed lower above ground biomass in the browsed treatment than the unbrowsed treatment, only rowan above ground biomass was significantly affected by moose browsing. Although Spruce and juniper showed higher above ground biomass in the browsed treatment, the interaction effect of treatment over year was not statistically significant.

Moose browsing significantly affected the above ground C- stock in the study sites. Based on the result at the end of the study, the browsed treatment showed lower mean above ground C stock than the unbrowsed treatment.

The current study confirmed that the presence of moose had negative impact on biomass of rowan and total above ground C-stock in Norwegian boreal forests. These findings show the importance of herbivory during forest C stocks management.

Key words: boreal forest, moose browsing, above ground biomass, above ground carbon stock,

Table of Contents

List of Tables

List of Figures

List of Appendices

List of Abbreviations

AGB= above ground biomass

Above ground C stock= above ground carbon stock

1. INTRODUCTION

1.1 Background

The boreal forest is the largest continuous forest ecosystem on the globe. It covers about 38% of world forest area and about14% of the vegetation surface of the earth. It is located in northern hemisphere Alaska, Fennoscandia, Canada, and Russia. It situated with approximate latitude of between 45 and 70^{o}north (Soja, 2007).

In boreal forest ecology, cold winters and deep snow-cover are common features (Tivy, 1993). It is habitat to large browsing and grazing mammals such as moose (Alces alces) and deer (Bryant and Chapin 1986). In terms of plant species, boreal forest consists different conifer genus such as fir (*Abies*), pine (*Pinus*), larch (*Larix*), juniper (*Juniperus*) and spruce (*Picea*). In addition to this, a number of deciduous plant genus such as rowan (*Sorbus*), aspen (*Populus*), birch (*Betula*), willow (*Salix*), and alder (*Alnus*) live in this environment. (Kinnunen, R et al. 2013).

Disturbance is any discrete event that alters the vegetation and creates new opening space for colonization (Edenius et al., 2002). This allows for new plants to emerge and succession to take place. Succession is a unidirectional change of community; in this process, the communities replace one another orderly until it reaches a more stable state (Small and Witherick, 1986). Moreover, forest succession is the process of change in the species composition, structure, and function of an ecological community over time. Early successional species often grow fast after disturbance, though they usually become outcompeted by the late successional species. Broadleaved deciduous plants are the early successional species and coniferous species are the late successional species in boreal ecosystem (Connell &Slatyer, 1977). There are many factors that affect forest succession. Based on the previous definition of disturbance, herbivory and forest clear-cutting can be considered as disturbance that can change the community (Edenius et al., 2002). The combined effect of herbivore browsing and forest clear-cutting has an impact on forest regeneration (Speed et al., 2013).

Moose is a common herbivore in boreal forests (Peterson, 1955). The moose population had a strong increase in Norwegian boreal forests especially during 1970-1990 (Austrheim et al., 2011). The bull consumes 7000-9000kg fresh biomass annually, of mainly shrubs and trees

(Persson, et. al. 2000). Selective browsing by moose can change the composition of woody plant communities. It increases the abundance of unpalatable species (Bryant& Chapin, 1986). For example, in the boreal forest browsing of poorly defended deciduous species such as willow (Salix spp.), aspen, and birch by moose favors more resistant evergreens such as white spruce (Bryant, et al.1980). Similarly, Speed et al. (2013) concluded that moose browsing have the tendency to change the community from deciduous species to coniferous species.

Biological, chemical and physical processes of the ecosystems can be mediated by animals as they affect carbon fixation and the amount of C transported to C reservoirs (Schmitz, et al., 2014). Due to their longevity and size, their habitat requirements and feeding strategies, large browsing mammals could possibly have a significant effect on ecosystem C storage (Rambo and Faeth, 1999). The direct effect of herbivores on the carbon stocks is through the consumption of vegetation, mainly leaves, and its metabolic conversion to methane and CO_2 (Hollinger & Hunt, 1990; Swainson et al. 2008). This result is also confirmed by Dyer (1980) who stated that herbivores can decreases fitness, growth, and survival of most plants species that are browsed. Reduction in biomass can result in decreasing above-ground carbon stocks. The above impacts of herbivores on carbon stocks are dependent on factors such as herbivore consumption rates, climatic conditions, primary productivity, and evolutionary histories (Milchunas & Laurenroth, 1993).

Carbon dioxide (CO_2) is the common form of carbon in the atmosphere. Even though it constitutes approximately 0.04% of the atmosphere, it plays a great role in supporting life. Plants use CO_2 for photosynthesis and convert it in to carbohydrate. This photosynthesis product plays a great role to maintain animal life. Moreover, when plants die the carbon stored in the plant return back to the atmosphere in the form of CO_2 following decomposition (Vashum and Jayakumar, 2012) or it becomes stored in the soil as soil organic carbon (Rodin & Basilevich 1965). Nowadays the emission of greenhouse gases such as carbon dioxide, methane and nitrous oxide has become a great concern due to global warming and other effects on living things (Yadava, 2010). The reason why the carbon cycle gets so much attention is because among global warming factors, 60% of the change is due to increasing CO_2 concentrations in the atmosphere (Grace, 2004). Moreover Lashof, and Dilip, (1990), indicated that among greenhouse gas emissions, CO_2 emission accounts 80% of the contribution to global warming.CO_2 concentrations can be reduced in the atmosphere by raising the rates of removal of CO_2 gas and increase the C storage within ecosystem C stocks. C storage is long term storage of C in the underground, terrestrial biosphere or the ocean. This slows or reduces the buildup of CO_2 concentration in the atmosphere (Yadava, 2010).

Plant biomass includes both aboveground and below ground parts of the plants. Trees and woody plants can accumulate high amounts of C throughout their lifespan (IPPC, 2006). Forest environments are the main reserves for terrestrial C stocks, (Malhi, et al. 1999). Total forest area is estimated to be around 30.6 % or 3999 million ha of the planet's land area (FAO, 2016). The global terrestrial ecosystems consist of approximately 1500 Pg (petagrams) of C stored in soils and 600 Pg of C in aboveground biomass (Reeburgh, 1997). Based on Pan et al. (2011), the current C stock in the world's forests is estimated to be 861 ± 66Pg C, with 363 ± 28 Pg C (42%) in live biomass (above and below ground), 383 ± 30 Pg C (44%) in soil (to 1-m depth), 73 ± 6 Pg C (8%) in deadwood, and 43 ± 3 Pg C (5%) in litter. Furthermore, in nature, 471 ± 93 Pg C (55%) is stored in tropical forests, 119 ± 6 Pg C (14%) in temperate forests and 272 ± 23 Pg C (32%) is stored in boreal forest. According to Martin Thurner1, et al., (2014) In 2010, the temperate and boreal forest ecosystems of the Northern Hemisphere stored 79.8 ± 29.9 Pg C and the mean C density was found 4.76± 1.78 kg Cm^{-2} of forest area. The unique cold climate condition of boreal forest is the main reason why this ecosystem play a great role for the storage of global terrestrial C, primarily in the below ground C stock of the forest (Apps et al., 1993; Alexeyev and Birdsey, 1998).

The amount of C stored in boreal ecosystem can be affected by different factors. Krefting, (1974) indicate that, the effects of herbivores on C stock are long lasting and potentially large. Based on (Schmitz,et.al. 2014) C storage in this ecosystem can decline in the presence of high number of moose. Moreover, according to Dyer (1980), moose can reduce above ground C stocks and prevent further sequestration through the consumption of vegetation. Changing species composition could change terrestrial C stock (Bunker, et al. 2005). In addition to this, selective feeding by moose can impact on C storage by decreasing the deciduous plant biomass. Therefore, the objectives of this study were to investigate the effect of browsing on above ground biomass and C stock, which is important to predict future climate change.

1.2 Study questions

Table 1. Study questions, hypothesis and mechanisms presented in table

Study question 1	Hypothesis (H1)	Mechanism 1	Reference
How does browsing affect successional development of plant biomass in Norwegian boreal forests.	Browsing will reduce the biomass increase of deciduous plants but not reduce biomass increase of conifer plants	Moose are Selective browsers they consume high nutritional plants	Bryant& Chapin, 1986
Study question 2	Hypothesis (H2)	Mechanism 2	Reference
How does browsing affect successional development of above-ground carbon stocks in Norwegian boreal forests.	Excusing moose will cause an increase above ground C stocks in boreal forest	Moose decreased above ground biomass which can lead to decrease in above ground carbon stock	Litton, et al., 2007

2. Method

2.1 The study area

The study was conducted in Trøndelag, central Norway. The common large herbivores in the study area are moose, red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*). Moose is the dominant herbivore at the study sites (Speed et al., 2013). Among the tree species, spruce, pine, juniper and different deciduous species such as birch, rowan, and goat willow are found at the study sites.

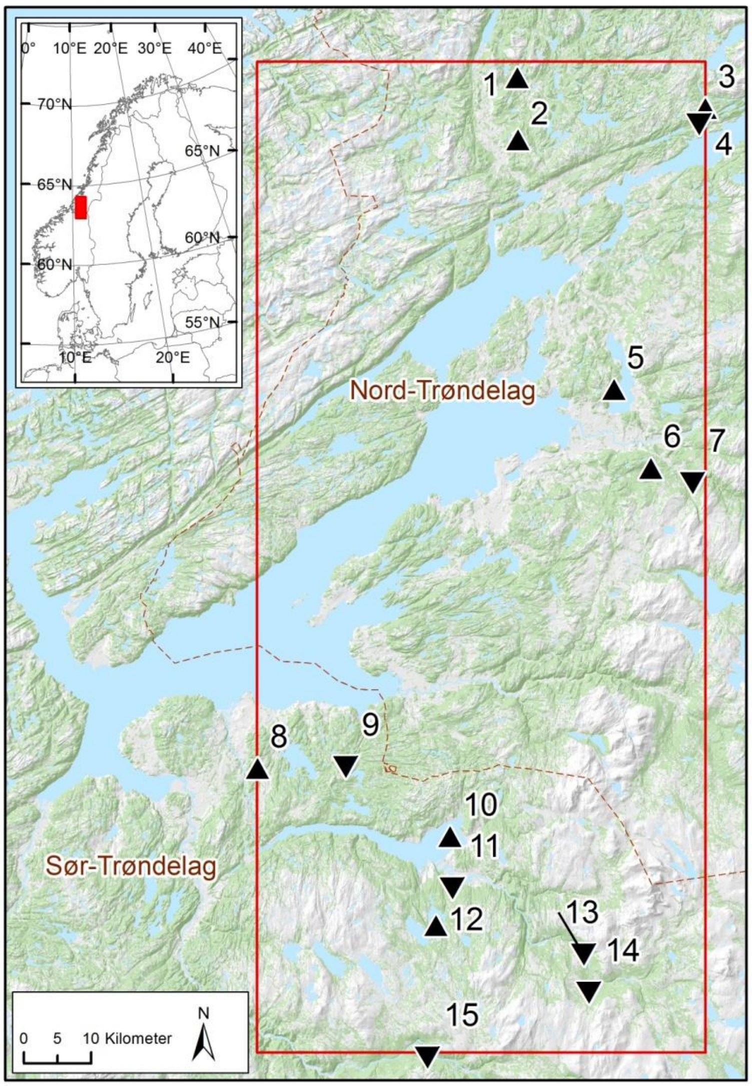

Figure 1. Location of the study sites.

2.2 Experimental design

To study the effects of herbivores on above ground carbon stocks,15 sites were selected on recently clear cut sites in Trøndelag in 2008 (Fig. 1). Two 20 x20 meters plots were randomly selected and assigned to exclosures treatment and unexclosed treatment. Plots were approximately 20 meter apart to help to minimize edge effects. The exclosure treatment had fences about 2.5 meters tall to prevent herbivores from entering. Each plot has four marked subplots with a radius of 2 meters and 12.5 m^2 total area (Speed et al. 2013). Trees (Norway spruce *(Picea abies)*, Scots pine *(Pinus sylvestris)*, rowan *(Sorbus)*, downy birch *(Betula pubescens)*, Juniper *(Juniperus)*, goat willow *(Salix caprea)* and silver birch *(Betula pendul*a) height (2009-2016), stem diameter at base (2016) were recorded in the spring from these subplots. Trees (downy birch, rowan, pine, spruce) of different sizes were harvested from outside the plots and some individuals of birch, rowan and pine were collected inside the exclosures treatment. For the calibration of the biomass models, trees with heights<50, 50-100 and <100 cm were selected using as stratified, random approach. The selection was randomized by throwing a stick over the back of a head and going wherever it lands. Afterwards, the closest trees of all species that grew near by the stick were cut close to ground level and transferred to the laboratory. When the necessary number of trees couldn’t be found in the first location another location was selected. To select another sample location, the same procedure was followed for all the selected sites (5 and 6, 8, 13,) (table 1) during July 2016.The four sites were selected based on their species diversity and geographical location (located far apart). A total of 132 samples (31 rowan, 48 downy birch, 26 pine, and 26 spruce) were randomly selected and harvested from outside the plots and 12 rowan, 1 birch and 1 pine inside the exclosures. The reason we harvested few trees inside the plot was in some sites we couldn’t find trees with the necessary height size outside the plot. Above ground parts of the plant such as stem and leaf were taken to measure carbon stocks of the exclosures treatment and unexclosed treatment. This harvest data was used to develop relationships between biomass and tree height by using quadratic regression.

The harvested above-ground vegetations were cut in small pieces and dried at 60^0C temperature in a drying cabinet for 48 hr for branches and leaves and 72 hr for stems. Following this, total dry biomass (stems + leaves + branches) of the plants were recorded. Weighing of the biomass was carried out in NTNU University Museum laboratory. The biomass model which are pine, spruce, downy birch, rowan browsed and rowan unbrowsed quadratic regression models were performed from the harvest data. The reason for using a separated model for rowan browsed and rowan unbrowsed was, because of growth variation between the two treatments. The unbrowsed treatments showed high growth variation. After this the biomass models were used to predict tree biomass from 2009-2016 for all species separately, and combined. Moreover, because of few numbers of goat willow and juniper in the study sites for harvesting, the downy birch model was used to predict goat willow biomass and spruce model was used to predict juniper biomass. Afterwards, the total biomass in the plots in each year was estimated. Based on Martin Thurner, et al., (2014) 48.8% of the total biomass of deciduous plants is a stored C and coniferous plants have 50.8% of stored C in their biomass. Therefore, to calculate C stock of all the predicted data a factor of 0.488 was used to convert biomass to carbon for the deciduous species and 0.508 for the coniferous species.

Table 2. Study sites

Site no	**Site name**	**Municipality**	**elevation**	**Year of clear-cutting**	**productivity**
1	Namdalseid_1kub	Namdalseid	123	2004	High
2	Verdal_1vb	Verdal	229	2005	low
3	Steinkjer_1bbb	Steinkjer	252	2005	High
4	Steinkjer_2bbb	Steinkjer	158	2004	medium
5	Verdal_2vb	Verdal	202	2003	medium
6	Nsb_verdal	Verdal	127	2006	medium
7	Sub_namdalseid	Namdalseid	291	2006	High
8	Bratsberg	Trondheim	237	2002	medium
9	Hi_Tydal	Tydal	298	2005	medium
10	Malvik	Malvik	247	2002	medium
11	Selbu_Flub	Selbu	184	2004	High
12	Selbu_kl	Selbu	311	2002	low

13	Selbu_sl	Selbu	379	2003	medium
14	Singsås	Singsås	286	2005	low
15	Sl_tydal	Tydal	429	2005	medium

2.3 Statistical Analyses

All statistical analyses were performed with R-Studio version 3.2.2. To see the effect of browsing on above ground biomass and C-stock over time between the treatments, the predicted plot biomass from 2009-2016 was used. To avoid pseudo replication a mixed effect model was used. Site was used as a random effect to account for locality differences of the plants and to control for the paired design. Moreover the interaction of treatment and Year since exclosure were used as fixed effects because they are expected to affect biomass and C stock of the plants in predictable way. The nlme package was used for mixed effects modeling (speed, 2013). Response variables were log transformed to avoid heteroscedasticity.

2.4 Model selection

The dry biomass data from harvested sample was used to create pine, birch, spruce, rowan browsed and rowan unbrowsed model. Both the linear model and the quadratic model were performed and the results showed the quadratic model was the best model and has better multiple R^2 than the linear model. According to the summary the quadratic models showed multiple R^2 of 0.693 for pine model, 0.941 for birch model, 0.944 for spruce model, 0.716 for rowan browsed and 0.995 for rowan unbrowsed. Different models for browsed and unbrowsed data were used for rowan. This is because there was growth form variation between browsed and unbrowsed treatment.

3. Result

3.1 Effect of browsing on above ground biomass

Table 3 indicates, the effect of moose browsing varies for each species. We recorded different slope for the browsed and the unbrowsed treatment for each plant. According to table 4 all the deciduous plants recorded higher mean above ground biomass (AGB) in the unbrowsed treatments. However, only rowan was significantly affected by moose. Moreover, the interaction of treatment and year didn't show significant effect on conifer plants.

3.2.1 Effect of browsing on above ground biomass of deciduous plants

According to figure 2, the AGB of deciduous species increased throughout the study in all treatments. The difference between the two treatments is presented visually in figure 2. There was a significant interaction between treatment and year in determining the AGB of rowan (P-value = 0.001) (table 3). However, the interaction effect of treatment and year for birch (P-value = 0.108) and goat willow (P-value = 0.216) were not statistically significant.

The interaction between treatment and year had a significant effect on the AGB of rowan. According to table 3 the slope was different between treatments [browsed treatment 0.16, SE=±0.04, unbrowsed treatment [0.59, SE=±0.05 (±SE is the difference of the year and year x browsing treatment standard error), n= 240)]. There was an increase of 0.16, SE=±0.04 in AGB for the browsed treatment for every year and an increase of 0.59, SE ±0.05 in AGB for the unbrowsed treatment for every year. As described in table 3 in the first year of the study (2009), rowan showed a slightly higher mean of AGB, (0.29± 0.15 g/m^2 (mean±SE)) in browsed treatment than in the unbrowsed treatment (0.23±0.11 g/m^2 (mean±SE). After eight years of succession (2016) the mean significantly changed and recorded 2.02±0.49 g/m^2 (mean±SE) for browsed plot and 124.70± 39.80 g/m^2 (mean±SE) for unbrowsed plot.

Even though, AGB of birch was higher in the last year of the study in unbrowsed treatment than browsed treatment (Fig. 2), the interaction effect between year over treatment was statistically not significant (P-value of 0.1298) (table 3). AGB in browsed treatment increased annually by 0.40, SE=±0.05 and for unbrowsed 0.50, SE=± 0.06. Mean AGB of birch in the first year (2009) increased for browsed treatment from (3.32± 1.82 g/m^2) (mean±SE) and unbrowsed (2.84± 1.10g/m^2) (mean±SE) to 81.70±26.04 g/m^2 (mean±SE), 163.72±38.86g/m^2 (mean±SE) in the last year of the study (2016) respectively (table. 4).

Though AGB of goat willow was lower in the presence of moose in 2016, the effect of moose browsing over year was statistically not significant (P-value of 0.216). From table 3 we can see an annual increase in AGB for the browsed treatment (0.10, SE=±0.03) and unbrowsed treatment (0.59, SE=±0.05) in every year. For goat willow the first year of the succession recorded a mean of 0.18± 0.09 g/m^2 (mean±SE) for browsed treatment and a mean of 0.002±0.001 g/m^2 (mean±SE) for unbrowsed treatment. On the other hand, the last year of the study showed mean of 0.85±0.40 g/m^2 (mean±SE) and 4.91± 3.29 g/m^2 (mean±SE) for browsed and unbrowsed treatment respectively (table 4).

3.2.2 Effect of browsing on above ground biomass of coniferous plants

There was no effect of the interaction between treatment and year on any coniferous species. Pine annually increased by 0.22, SE=±0.05 in the browsed plot and annually increased by 0.23, SE=±0.07 in unbrowsed plot. Moreover based on table 3 mean AGB for pine in the browsed treatment increased from 2.39±0.69 g/m^2 (mean±SE) in 2009 to 56.69±29.05g/m^2 (mean±SE) in 2016. In the unbrowsed treatment, Mean AGB increased from 2.39±0.87 g/m^2 (mean±SE) in year one to133.27± 81.42 g/m^2 (mean±SE) in year eight. However, the p-value for the interaction between treatment over year was not significant (p=0.841).

The results presented in Table 3 revealed that for spruce AGB was increased by 0.38, SE =±0.05 every year in the browsed treatment. In the unbrowsed treatment AGB was increased by 0.39, SE =±0.04 in each year. There was an increase in mean AGB, from 24.19±10.23 g/m^2 (mean±SE) at the start of the study to 256.21±51.71 g/m^2 (mean±SE) at the end of the study in the browsed treatment and from 25.711± 8.588 g/m^2 (mean±SE) at the first year to 232.02± 40.44g/m^2 (mean±SE) at the last year in the unbrowsed treatment. Although the result showed that there is variation on AGB between treatments, the interaction effect between treatments over year was statistically not significant (P-value of 0.878).

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The other conifer plant was juniper; its AGB showed a slight variation between the treatments. AGB in the browsed treatment increased annually by 0.04, SE =±0.03 and the annual increment of AGB in the unbrowsed treatment recorded 0.03, SE =± 0.05. In table 3 the P-value for the interaction effect between year over treatment was 0.82 (statistically not significant). Mean AGB of juniper for browsed treatment increased from 6.24± 5.43 g/m^2 (mean±SE) in year one to10.57± 7.02 g/m^2 (mean±SE) in year eight. The increment for unbrowsed treatment was from 0.016±0.02 g/m^2(mean±SE) at the first year of the study to 0.51± 0.49 g/m^2 (mean±SE) at the end of the study. Mean AGB in the browsed plot showed higher amount of biomass than the unbrowsed plot at the end of the study (table 4).

Table 3. The estimated effect and standard error of year and the interaction between treatment and year on the biomass for each species

Species		Coefficient	SE	DF	T-value	P-value
Rowan	Year	0.16	0.04	222	4.25	0.0001*
	Year x Browsing treatment	0.43	0.054	222	7.95	0.0001*
Birch	Year	0.4	0.05	222	8.77	0.0001*
	Year x Browsing treatment	0.10	0.06	222	1.61	0.108
Goat willow	Year	0.10	0.03	222	8.77	0.0001*
	Year x Browsing treatment	0.06	0.05	222	1.24	0.216
Pine	Year	0.22	0.05	222	4.15	0.0001*
	Year x Browsing treatment	0.07	0.07	222	0.35	0.841
Spruce	Year	0.37	0.04	222	10.65	0.0001*
	Year x Browsing treatment	-0.01	0.05	222	-0.153	0.878
juniper	Year	0.04	0.03	222	1.20	0.23
	Year x Browsing treatment	-0.011	0.05	222	-0.226	0.82

Browsed is the reference level for the browsing treatment factor. The coefficient for year can be interpreted as the slope of [biomass] increase for the browsed treatment. The slope for the unbrowsed treatment can be estimated from the addition of the coefficients of year and the interaction of year and treatment. The standard error for the unbrowsed treatment can be *calculated from the difference of the SE of year and the interaction of year and treatment. DF and* T-value *for year can be interpreted DF and* T-value *for the browsed treatment and The asterix (*) indicate significant variables (p<0.05)*

Table 4. *Mean and standard error of above ground biomass (g/m^2) of rowan, birch, goat willow, pine, spruce, and juniper plants in 2009 (first year of the study) and 2016 (last year of the study).*

[Species	Treatment	Year	Mean ± SE of above ground biomass (g/m^2)
Rowan	browsed	2009	0.29 ± 0.15
	unbrowsed	2009	0.23 ± 0,11
	browsed	2016	2,02±0,49
	unbrowsed	2016	124,7±39,8
Birch	browsed	2009	3,32±1,82
	unbrowsed	2009	2,84±1,103
	browsed	2016	81,7±26,04
	unbrowsed	2016	163,72±38,86
Goat willow	browsed	2009	0,18±0,09
	unbrowsed	2009	0,002±0,001
	browsed	2016	0,85±0,4
	unbrowsed	2016	4,91±3,29
Pine	browsed	2009	2,39±0,7
	unbrowsed	2009	2,39±0,87
	browsed	2016	56,69±29,05
	unbrowsed	2016	133,27±81,42
spruce	browsed	2009	24,19±10,23
	unbrowsed	2009	25,71±8,59
	browsed	2016	256,21±51,71
	unbrowsed	2016	232,02±40,44

Juniper	browsed	2009	6,24±5,43
	unbrowsed	2009	0,02±0,01
	browsed	2016	10,57±7,02
	unbrowsed	2016	0,51±0,49

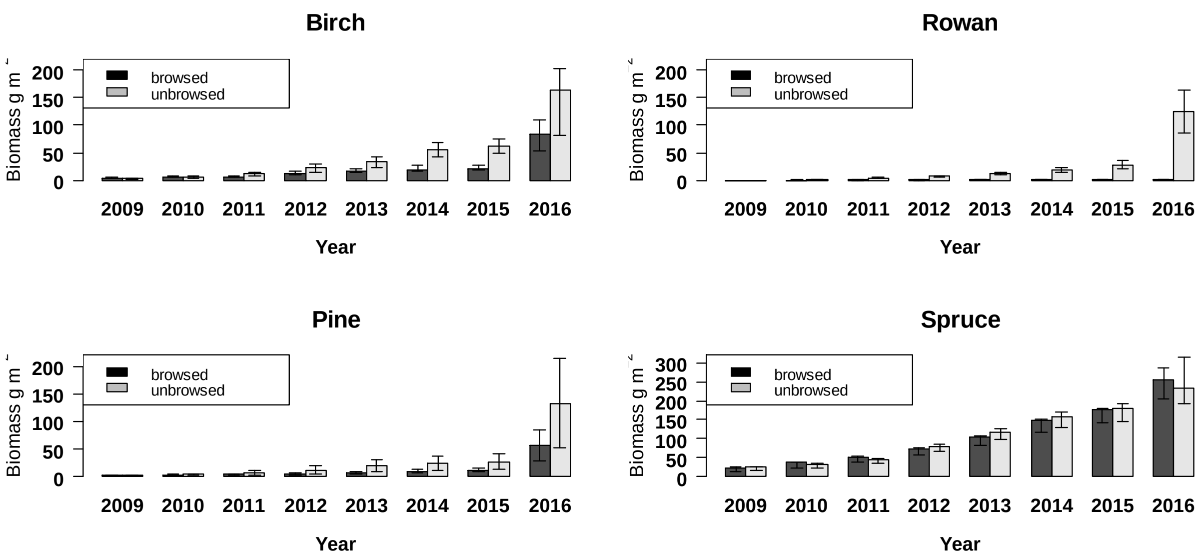

Figure 2. graphs for above ground biomass (g m^2) against year for each species of browsed (black) and unbrowsed (gray) treatment.

3.2 Effect of browsing on above ground carbon-stocks

The results of Table 4 have indicated that there was a significant effect of treatment and year on above ground C stock, the unbrowsed treatment showed higher amount of C stock than the browsed treatment at the end of the study (Fig 3). There was an increase in mean above ground biomass, from 74.10± 22.51g m^2 (mean±SE) at the first year of the study to 822.36± 140.74g m^2 (mean±SE) at last year of the study in the browsed treatment and from 63.12±17.64 g m^2 (mean±SE) at the start of the study to 1315.88± 195.33 g m^2 (mean±SE) at the end of the study in the unbrowsed treatment. The interaction effect between treatments over year had P-value of 0.0066.

Table 5. Table 4: Mean and standard error of above ground C-stock (g/m^2) of all species in 2009 and 2016

Species	Treatment	Year	Mean ± SE of above ground C stock (g/m^2)
All species	Browsed	2009	74,12±22,51
	Unbrowsed	2009	63,12±17,64
	Browsed	2016	822,36±140,74
	Unbrowsed	2016	1315,88±195,33

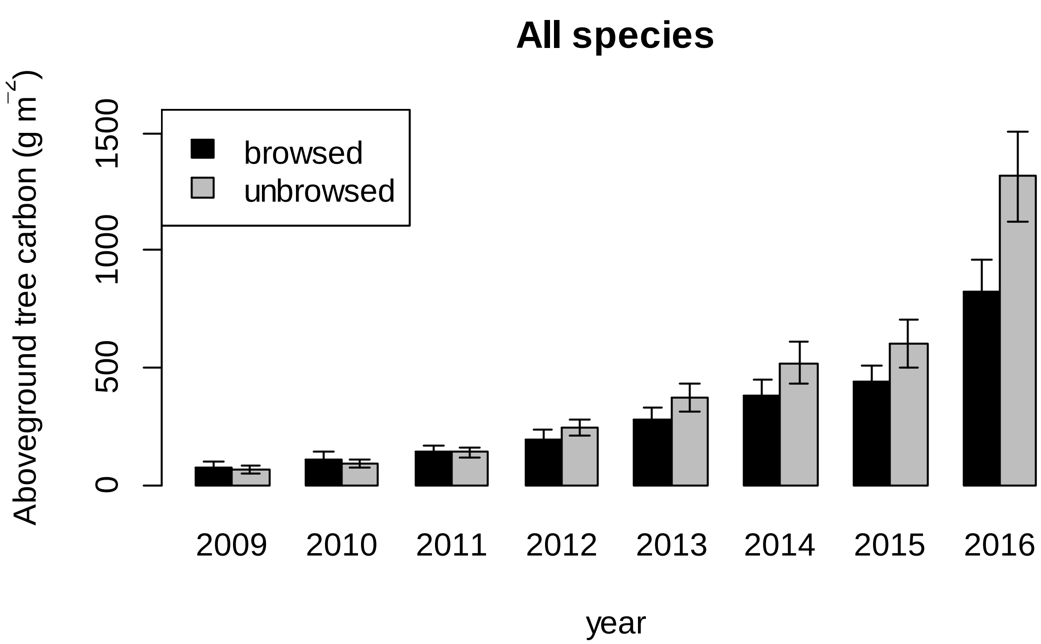

Figure 3. graph for total above ground carbon stocks against year of browsed (black) and unbrowsed (gray) treatment.

4. Discussion

Herbivores are usually found to have a strong top-down control on ecosystems (Skarpe & Hester, 2008). However, their effects on AGB and C stock have not been much studied. To examine the effect of moose browsing on AGB and C stock an exclosure study was performed in Norwegian boreal forests in central Norway.

To investigate the effect of moose, the predicted biomass and C stock data were compared between browsed and unbrowsed treatment. As predicted we recorded a significant difference of rowan AGB between treatments. For the other deciduous plant, we failed to record significant effect of moose browsing on AGB in seven years of succession. Furthermore, we documented that moose didn't significantly change AGB of conifer plants. As predicted in our (H_2), lower above ground C stock showed in the browsed than unbrowsed treatments.

According to Bagchi and Ritchie, (2010) large herbivores could cause neutral, positive or negative effects on AGB in different ecosystems. Cui et al. (2005) showed that in the grazed plot AGB decreased by 65–79% within 25 years in Mongolia. Similarly, Köster, (2013) found that AGB decreased in the presence of reindeer in a boreal forest ecosystem. The number of trees in the closed plot was 2675 ha^{-1} and 1100 ha^{-1} in the open plot. The mechanisms how herbivores reduce AGB can be through directly consumption or debarking. Nomiya, et al (2003) showed that debarking by deer directly decreased woody plant biomass in deciduous forest.

4.1 Deciduous plants

Due to selective browsing by moose, we expected the presence of moose has an impact on the AGB of deciduous plants. After eight years of the clear cut, AGB of deciduous plants increased in both treatments. The unbrowsed treatment showed higher slope than the browsed treatment for all the deciduous species (table 3). This implies the annual increment of AGB in the unbrowsed treatment was higher than the browsed treatment. In table 4 we can observe lower AGB of deciduous plants when they exposed to browsing. The reason for that deciduous plants contain different important nutrients and have weak defense mechanism compare to conifer plants (Bryant& Chapin, 1986; Bryant, et al.1980). Moreover, Tolerance strategies of deciduous plants to resist herbivory can have a negative impact on biomass. According to Mathisen, (2017) some tolerance strategies increase susceptibility for browsing. For example, rapid regrowth of deciduous plants to resist herbivory increases the palatability of new shoots. Likewise, DuToit, (1990) explain that rapid regrowth leads to more nutritious shoots by reducing the synthesis of secondary metabolites. Furthermore, based on a review by Skarpe and Hester (2008) tolerance strategies of plants have a positive impact for herbivoiry browsing. It can increase resource availability and quantity of palatable plants in the area. Bergqvist et al., (2003) discussed the feeding loop concept which implies that herbivore has the highest probability to consume on previously browsed plants or patches than on unbrowsed plants.

Even though all deciduous plants showed a difference of AGB between treatments, the result indicates moose has a significant effect on rowan plant only. Similarly, Hörnberg, (1995) observed that in the presence of moose there was a lower increase in browsed than unbrowsed treatment of rowan, aspen and other preferred species between the years 1969–72 and 1983–87. Likewise, Angelstam et al. (2000) recorded that the cover of rowan, goat willow, and aspen were strongly negatively associated with moose density. Although, some researcher observed a significant effect of moose on goat willow biomass (Angelstam et al. 2000), we fail to record statistical significant difference of goat willow AGB. The reasons why we did not see a significant effect of moose browsing on above ground biomass of goat willow might be due to the shortage of data. There were few trees of goat willow in the study site. The total data might not be enough to see the interaction effect of treatment and year over AGB of goat willow. This study included 7 years' data of the succession after treatment. Even if, we didn't see statistical significant difference of AGB in all deciduous plants, we will probably see a significant reduction of AGB in all the deciduous preferred plants in future studies.

4.2 Conifer plants

Based on our prediction, we didn't expect to see an effect of moose browsing on terrestrial AGB of coniferous plants. When AGB of conifer plants compared from the start to the end of the study, we can observe mean AGB increased for all conifer plants.

The interaction of treatment over year did not influence the AGB of conifer plants. This is because conifer plants are more resistant and have low available nutrition (Skarpe & Hester, 2008). Moreover, conifer plants have a strong structural defense mechanism that can prevent moose from debarking. Also, these species have a strong chemical defense which can decrease digestibility, test or be being toxic (Bryant et al, 1991; Davidson, 1993). Moreover, Weber et al., (2008) explain that herbivory has a little effect on biomass of less herbivore palatable and browse tolerant species. As predicted, moose didn't show a significant effect on all coniferous plants. However, there was some variation of AGB between treatments. Pine showed higher mean AGB in the unbrowsed treatment. The reason why we observed higher mean for pine might be during winter season moose faces shortage of food supplies; fresh leaves and buds of preferred deciduous plants are not available. To avoid food problem during this season, moose might browse pine among the ever-green conifer plants. Hjeljord and Härkönen, (2014) confirmed that Scandinavian moose consume pine in winter season. Our result indicated that spruce and juniper had higher mean above ground biomass in the browsed treatment. This can be because of their strong structural and chemical defense for herbivory. Moreover, since the other plants (rowan, birch, goat willow and pine) showed lower biomass in the browsed treatment, this might decrease competition and accelerate spruce and juniper growth in the open plot. We can state that spruce and juniper species are the least preferred plants for moose browsing. This finding will give important information for forest land owners who believe moose browsing has a negative effect for their spruce production. Similarly, this result is supported by Heikkila et al. (2003) that observed more spruce biomass in the browsed plot.

4.3 Above ground C stock

In recent time, various human activities are responsible for the rising of CO_2 concentration and global warming. Forest ecosystems are the main reservoirs for C storage and play an essential role to balance atmospheric CO_2. C stock in the forest can be affected by the presence of moose (Schmitz,et.al. 2014). Our results support H_2. It clearly indicated that moose can significantly decrease above ground C stock in boreal forests. The result indicates from the first year of the study to the last year of the study above ground C stock in the browsed and unbrowsed treatment was increased. From table 5 we can see the unbrowsed treatment showed higher amount of C stock than the browsed treatment. The reason for that moose reduced aboveground biomass in the browsed plot that can be used for storage of carbon. This reason was discussed by Litton, et al (2007) herbivores consumption of above-ground biomass results reduction of terrestrial C stocks. Likewise,`the above result was confirmed by Tanentzap & Coomes, (2012) excluding herbivores will decrease consumption of plant biomass, this will increases above ground C stocks across vegetation types through time. Similarly Schmitz,et.al. (2014) discussed that moose can negatively affected C storage in boreal ecosystem. This is because moose can decrease canopy height by directly consuming photosynthetic tissue of the plants. According to Kunstler & Coomes, (2007) herbivory decreased above ground C stock, moreover they might also delay the accumulation of C stock. This is because herbivory consume less resistance, fast grower species. The plants that have more resistant to herbivory most of the time grow slowly which delay C accumulation in the plant. Based on Our result of 2009 and 2016 we also confirmed plant successional year and the presence of moose significantly affected above ground C stock.

5. Limitation of the study

The aim of this study is to investigate the effect of moose browsing on above ground biomass and above ground C stock in Norwegian boreal forests. The significant effect of moose depends on different factors such as productivity and moose density (speed, 2013). Bergman, (2002) indicated low level of herbivory has a positive effect for plants by stimulating regrowth and increase biomass. Based on Angelstam et al. (2000) finding the effect of moose on above ground biomass of deciduous plant increased when density of the moose became high. In this study productivity and moose density data of the 15 study sites were not included. Therefore, the significant effect of moose browsing in our result may not the same for all the study sites; instead it clearly showed the average effect of moose in the study sites.

6. Relevance of the study

In Earlier studies the impact of herbivory on above ground C stock had low consideration than the other factors. The result of this study showed how moose browsing can decrease above ground biomass and C stock in Norwegian boreal forests. Similarly Litton, et al 2007; Schmitz,et.al. 2014 indicated the importance of herbivory in forest C stock management. Furthermore, this study confirms moose has different effect on biomass of different plants. According to the result moose decreased above ground biomass of rowan. The result will be important for plant conservation in boreal ecosystem.

7. Conclusion

This study confirms the following Overall conclusions.

- All the deciduous plants and pine showed lower amount of AGB in the browsed treatment. On other hand, the conifer plant juniper and spruce recorded higher biomass in the browsed treatment. Although there was a variation of AGB between treatments for all plants, Moose browsing only showed a significant effect on rowan.
- The presence of moose had a negative effect on above ground C stocks. This indicates herbivory effect should be considered for forest C stocks management.

8. Recommendation

Suggested recommendations for future study based on the above conclusion are:

To get a statistical significant effect of moose on AGB and C stock in sucssetional forests, long term studies needed. The SUSTHERB project is ongoing project therefore we will probably see a significant effect of moose browsing on above ground biomass in all the preferred plants.

This study was not cover all boreal forests of the country; therefore, further studies must be conducted on the effect of moose browsing from other area of Norwegian boreal forests. Large scale approach is needed.

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10. Reference

Apps, M. J., Kurz, W. A., Luxmoore, R. J., Nilsson, L. O., Sedjo, R. A., Schmidt, R., ... & Vinson, T. S. (1993). Boreal forests and tundra. In *Terrestrial Biospheric Carbon Fluxes Quantification of Sinks and Sources of CO2* (pp. 39-53). Springer Netherlands.

Alexeyev, V. A., & Birdsey, R. A. (1998). Carbon storage in forests and peatlands of Russia. USDA For. *Serv. Northeastern Res. Statn., Radnor, Penn. Gen. Tech. Rep. NE-244.[Initially published in Russian in 1994]*.

Angelstam, P., Wikberg, P. E., Danilov, P., Faber, W. E., & Nygren, K. (2000). Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. *Alces*, 133-146.

Austrheim, G., Solberg, E. J., & Mysterud, A. (2011). Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology, 17*(3), 286-298. doi: 10.2981/10-038

Bagchi, S., & Ritchie, M. E. (2010). Herbivore effects on above-and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes. *Oecologia*, *164*(4), 1075-1082.

Bee, J. N., Kunstler, G., & Coomes, D. A. (2007). Resistance and resilience of New Zealand tree species to browsing. *Journal of Ecology*, *95*(5), 1014-1026.

Bergman, M. (2002). Can saliva from moose, Alces alces, affect growth responses in the sallow, Salix caprea?. *Oikos*, *96*(1), 164-168.

Bergqvist, G., Bergström, R., & Edenius, L. (2003). Effects of moose (Alces alces) rebrowsing on damage development in young stands of Scots pine (Pinus sylvestris). *Forest Ecology and Management*, *176*(1), 397-403.

Bryant, J. P., & Chapin III, F. S. (1986). Browsing-woody plant interactions during boreal forest plant succession. In *Forest ecosystems in the Alaskan taiga* (pp. 213-225). Springer New York.

Bryant, J. P., Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry, Annu. Rev. Ecol. Syst. 11:261-85

Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P., & du Toit, J. T. (1991). Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, *22*(1), 431-446.

Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O. L., &Naeem, S. (2005). Species loss and aboveground carbon storage in a tropical forest. *Science*, *310*(5750), 1029-1031.

Connell, J. H., &Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, *111*(982), 1119-1144.

Cui, X., Wang, Y., Niu, H., Wu, J., Wang, S., Schnug, E., ... & Tang, Y. (2005). Effect of long-term grazing on soil organic carbon content in semiarid steppes in Inner Mongolia. *Ecological Research*, *20*(5), 519-527.

Davidson, D. W. (1993). The effects of herbivory and granivory on terrestrial plant succession. *Oikos*, 23-35.

Dyer, M. I. (1980). Mammalian epidermal growth factor promotes plant growth. *Proceedings of the National Academy of Sciences*, *77*(8), 4836-4837.

DuToit, J. T., Bryant, J. P., & Frisby, K. (1990). Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. *Ecology*, *71*(1), 149-154.

Edenius, L., Bergman, M., Ericsson, G., & Danell, K. (2002). The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica*, *36*(1), 57-67.

FAO (2016), global forest resources assessment, rome.

Grace, J. (2004). Understanding and managing the global carbon cycle. *Journal of Ecology*, *92*(2), 189-202

Heikkila, Risto, Pertti Hokkanen, Mira Kooiman, Nilay Ayguney, and Cyril Bassoulet. "The impact of moose browsing on tree species composition in Finland." *Alces* 39 (2003): 203-214.

Hollinger, D. Y., & Hunt, J. E. (1990). Anthropogenic emissions of carbon dioxide and methane in New Zealand. *Journal of the Royal Society of New Zealand*, *20*(4), 337-348.

Hörnberg, G., Ohlson, M., & Zackrisson, O. (1995). Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth Picea abies swamp-forests. *Journal of Vegetation Science*, *6*(2), 291-298.

IPCC. (2006). Guidelines for National Greenhouse Gas Inventories. Available online at www.ipccnggip. iges.or.jp/public/2006gl/index.html

Kinnunen, R., Lehtonen, I., Kas, J., Järvelä, R., Poutamo, H., Wenzlaff, C., & Latus, J. (2013) Impact of Climate Change on the Boreal Forest in Finland and Sweden.

Köster, E., Köster, K., Aurela, M., Laurila, T., Berninger, F., Lohila, A., & Pumpanen, J. (2013). Impact of reindeer herding on vegetation biomass and soil carbon content: a case study from Sodankylä, Finland. *Boreal Environment Research*.

Krefting, L. W., Bedard, J., Telfer, E. S., Wolfe, M. L., Peek, J., Simkin, D. W., ... & Ritcey, R. W. (1974). Moose distribution and habitat selection in north central North America.

Lashof, Daniel A., and Dilip R. Ahuja. "Relative contributions of greenhouse gas emissions to global warming." *Nature* 344.6266 (1990): 529-531.

Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, *13*(10), 2089-2109.

Malhi, Y., Baldocchi, D. D., & Jarvis, P. G. (1999). The carbon balance of tropical, temperate and boreal forests. *Plant, Cell & Environment*, *22*(6), 715-740.

Mathisen, K. M., Milner, J. M., & Skarpe, C. (2017). Moose–tree interactions: rebrowsing is common across tree species. *BMC ecology*, *17*(1), 12.

Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological monographs*, *63*(4), 327-366.

Nomiya, H., Suzuki, W., Kanazashi, T., Shibata, M., Tanaka, H., & Nakashizuka, T. (2003). The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. *Plant Ecology*, *164*(2), 263-276.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., ... & Ciais, P. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045), 988-993.

Persson, i.-l., danell, k. &bergström, r. Disturbance by large herbivores in boreal forests with special reference to moose. Annaleszoologicifennici, 2000. Jstor, 251-263.

Peterson, R. L. (1955). North American Moose University of Toronto Press. *Toronto, Ontario, Canada*.

Rambo, J. L., &Faeth, S. H. (1999). Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology*, *13*(5), 1047-1054.

Rea, R. V., Hjeljord, O., & Härkönen, S. (2014). Differential selection of North American and Scandinavian conifer browse by northwestern moose (Alces alces andersoni) in winter. *Acta theriologica*, *59*(2), 353-360.

Reeburgh, W. S. (1997). Figures summarizing the global cycles of biogeochemical important elements. *Bulletin of the Ecological Society of America*, 260-267.

Rodin, L. E., & Basilevich, N. I. (1965). Dynamics of organic matter and biological turnover in the most important vegetation types.

Schmitz, O. J., Raymond, P. A., Estes, J. A., Kurz, W. A., Holtgrieve, G. W., Ritchie, M. E., ... & Christensen, V. (2014). Animating the carbon cycle. *Ecosystems*, *17*(2), 344-359.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., ... & Stackhouse, P. W. (2007). Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change*, *56*(3), 274-296.

Skarpe, C., & Hester, A. J. (2008). Plant traits, browsing and gazing herbivores, and vegetation dynamics. In *The ecology of browsing and grazing* (pp. 217-261). Springer Berlin Heidelberg.

Small, J., and Witherick, M. (1986). A Modern Dictionary of Geography. Edward Arnold, London.

Speed, J. D., Austrheim, G., Hester, A. J., Solberg, E. J., & Tremblay, J. P. (2013). Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. *Forest Ecology and Management*, *289*, 289-299.

Speed, J. D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø.,&Austrheim, G. (2014). Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem.*Ecosystems*, *17*(7), 1138-1150.

Swainson NM, Hoskin SO, Clark H, Pinares-Patino CS, Brookes IM 2008. Comparative methane emissions from cattle, red deer and sheep. Proceedings of the Deer Branch of the New Zealand Veterinary Association 68: 59–62.

Tivy, J. 1993Biogeography. A study of plants in the ecosphere. Longman Scientific & Technical, UK.If global mean temperature in the 21st century increases by 2.8oC, most of the boreal forest belt will experience 4-5oC warming.

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72-94.

Thurner, M., Beer, C., Santoro, M., Carvalhais, N., Wutzler, T., Schepaschenko, D., ... & Schmullius, C. (2014). Carbon stock and density of northern boreal and temperate forests. *Global Ecology and Biogeography*, *23*(3), 297-310.

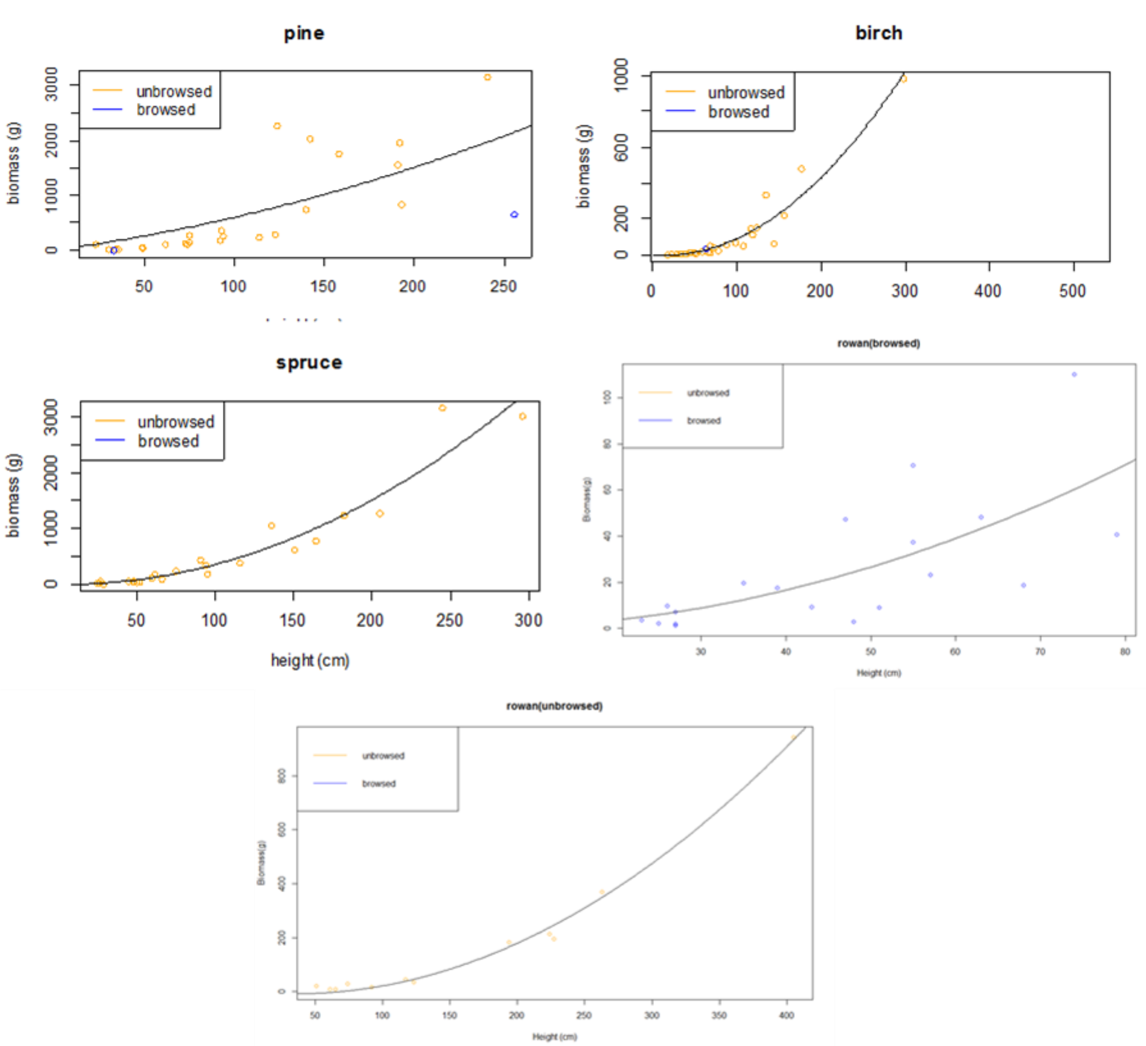
Vashum, K. T., &Jayakumar, S. (2012). Methods to estimate above-ground biomass and carbon stock in natural forests-a review. *Journal of Ecosystem &Ecography*, *2*(116), 1-7.

Weber, P., Rigling, A., & Bugmann, H. (2008). Sensitivity of stand dynamics to grazing in mixed Pinus sylvestris and Quercus pubescens forests: a modelling study. *ecological modelling*, *210*(3), 301-311.

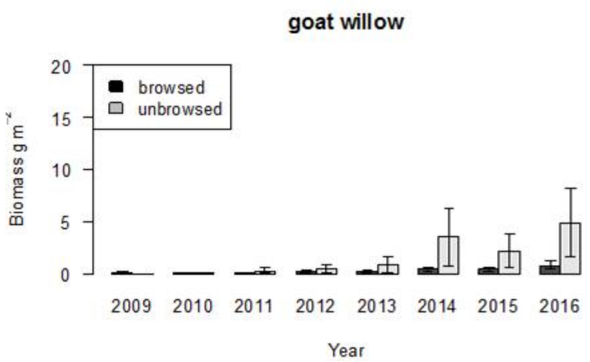
Yadava, A. K. (2010). Carbon sequestration: underexploited environmental benefits of Tarai agroforestry systems. *Indian Journal of Soil Conservation*, *38* (2), 125-131.

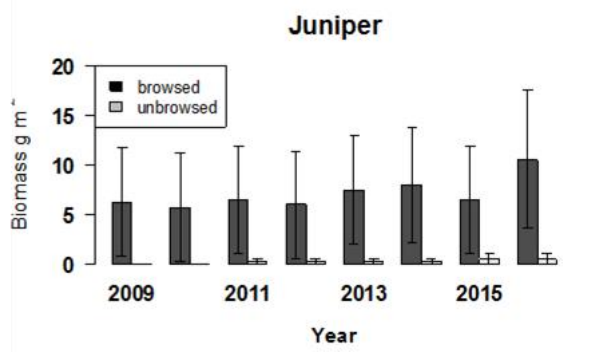
11. Appendix

Appendix 1. Graphs of pine, birch, rowan browsed, rowan unbrowsed and spruce models



Appendix 2. Graphs for above ground biomass (g m^2) against year for juniper and goat willow of browsed (black) and unbrowsed (gray) treatment.





Appendix 3 table for total above ground C stock (g m^2) from 2009 to 2016.

Species	Treatment	Year	Mean ± SE of above ground C stock (g/m^2)
All species	Browsed	2009	74,12±22,51
	Unbrowsed	2009	63,12±17,64
	Browsed	2010	107.59±32.01
	Unbrowsed	2010	89.68±17.64
	Browsed	2011	139.50±30.88
	Unbrowsed	2011	137.71±21.88
	Browsed	2012	194.61±39.28
	Unbrowsed	2012	243.96±38.04
	Browsed	2013	276.87±53.25
	Unbrowsed	2013	369.78±58.71
	Browsed	2014	519.77±69.55
	Unbrowsed	2014	369.78±89.34
	Browsed	2015	439.08±66.67
	Unbrowsed	2015	600.70±100.53
	Browsed	2016	822,36±140,74
	Unbrowsed	2016	1315,88±195,33