Browsing on naturally regenerated oak seedlings: the interaction between cervid browsing and light availability

Photo: Linda Petersson

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Master Thesis no. 299

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Preface

I would like to thank my supervisor Linda Petersson for her guidance throughout the whole thesis process. Also, I would like to thank her for letting me use data from her project making this study possible. Furthermore, I would like to send a great thanks to my assistant supervisor Annika Felton for contributing with inputs and ideas to the study.

Abstract

Browsing on oak seedlings and other tree species is a major problem when regenerating forest in Sweden. Several factors such as light, surrounding vegetation and season, can influence browsing intensity and browsing frequency. In this study the relationship between cervid browsing and light was examined. Five sites were selected, three in Hornsö (Kalmar county), one in Halmstad (Halland county) and one in Sösdala (Skåne county), and in each site four plots were marked in the spring of 2016. The plots were assigned two light treatments, low and high light, and one plot in each light treatment was fenced. To analyse the data a linear mixed regression model was used.

Light had no significant effect on neither browsing intensity nor browsing frequency. The time of year, however, was shown to have a significant effect on browsing frequency and browsing intensity. Browsing frequency was the highest in winter and early spring. The lack of significance from light could be explained by the surrounding landscape and the low availability of palatable tree species. Habitat selection and difference in dietary choices could explain the increased browsing frequency on oak seedlings in winter and early spring. Cervids browse differently on oak seedlings depending on season and made no choice between oaks grown in high light or low light. Further studies on food quality selectivity in relation to food abundance are needed.

Keywords*: browsing intensity, browsing frequency, forest regeneration, moose, Quercus robur, roe deer, southern Sweden*

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Introduction

Browsing on seedlings and saplings is a major problem when regenerating forest (Gill 1992; Reimoser and Gossow 1996; Götmark et al. 2005). Some tree species are more preferred by herbivores which can give non-preferred tree species an advantage during regeneration (Gill 1992). This, in combination with large populations of wild cervids (Wallgren 2016) and a large proportion of standing forest represented by non-palatable species (Skogsdata 2018), has made it difficult both for forest plantation and natural regeneration of preferred species to establish and compete with the surrounding vegetation.

Certain environmental aspects, time of year, and location influence browsing (Kullberg and Bergström 2001; Kuijper et al. 2009; Bergqvist et al. 2018). Surrounding vegetation and site conditions can influence the amount of browsing damage on an individual seedling. For example, shrubs that grow together with palatable tree species can repel herbivores either through their physical defense or chemical properties (Perea & Gil 2014; Jensen et al. 2012a). The theory is that it becomes less probable for tree species to be browsed when they are growing within or in the presence of shrubs, as long as the tree seedlings do not overtop the protecting environment and thereby expose themselves to the risk of browsing (Jensen et al. 2012a). Although surrounding vegetation can reduce the risk of browsing it also changes the light conditions, which can be crucial for survival of some tree species (Götmark 2007; Jensen and Löf 2017). In addition to affecting the tree's survival rate, light conditions created by canopy openness also influence the growth rate of trees (Götmark 2007). Seedlings that have a higher growth rate can become more resilient to browsing, being more vigorous than seedlings growing in the shade (Baraza et al. 2004. A study in Bialowieza forest, Poland, discovered that cervids spend more time in forest gaps, with more light, than in closed forest when feeding (Kuijper et al. 2009). Damage due to browsing by rodents can also be higher in forest gaps than in closed forest. Kupferschmid et al. (2014) showed a higher likelihood of mouse browsing on silver fir (*Abies alba*) in forest gaps due to the increased amount of ground vegetation.

Browsing can also be dependent on the season. Diets of herbivores living at northern latitudes vary over the year depending on available food sources (Tixier & Duncan 1996; Moser et al. 2008). For example, fallow deer (*Dama dama*) in Great Britain showed different feeding preferences depending on time of the year. Feeding on trees increased during spring and into early summer, and then decreased again in late summer and into the fall (Moore et al. 2000). Similar results have been shown for roe deer (*Capreolus capreolus*) where forage selection is dependent on the season (Moser et al. 2008). Closely connected with food selection, habitat utilization by cervids also varies with the season (Massé and Côté 2012). For example, moose (*Alces alces*) in Sweden feeds on different tree species substantially in different land areas and feeding is highly proportional to the available forage in that landscape (Bergqvist et al. 2018). The browsing pressure on preferred tree species increases in winter when other food sources are less abundant (Moser et al. 2006; Månsson et al. 2007).

Cervids are selective in their food choice, which creates a disadvantage for plants that are more commonly browsed against vegetation that is less browsed. The risk of browsing damage is connected to a tree species palatability and the preference of herbivores (Gill 1992; Kullberg and Bergström 2001; Götmark et al. 2005). Why one tree species is more palatable than another could be explained through different survival strategies evolved over time. Species that initially grow slowly often have some kind of defence mechanism, either physical or chemical, making them less attractive to feed on (Bryant et al. 1983). On the other side of the spectra, species with initially fast growth rate allocate their energy on growing tall quickly to escape high risk browsing height. Therefore, fast growing species are more likely to be browsed compared to species with different survival strategies (Bryant et al. 1983). However, initial growth is only one of the factors that determine likelihood of browsing. Nutritional values seem to play an important role when it comes to selectivity in herbivores feeding behaviour (Stolter et al. 2013; Felton et al. 2018). Red deer (*Cervus elaphus*) have been shown to choose food patches with the most energy and nutrient rich forage (Langvatn & Hanley 1993; Gross et al 1993; Wilmshurst & Fryxell 1995). A similar pattern has been found for moose that choose to feed on seedlings in fertilized sites more than seedlings in non-fertilized sites (Ball et al. 2000). Additionally, the morphology of plants affects likelihood of browsing (Stolter et al. 2013). This means that plants that grow with favorable site conditions are more often browsed by cervids (Hartley et al. 1997). These findings suggest that cervids do select their food based on the nutrient content (Langvatn & Hanley 1993; Gross et al. 1993; Wilmshurst & Fryxell 1995; Hartley et al. 1997; Ball et al. 2000).

In comparison with many other tree species in the temperate region, both conifers and broadleaves, oaks (*Quercus spp.*) are highly preferable as food for herbivores (Götmark et al. 2005). For example, pedunculate oak (*Quercus robur*) shows higher susceptibility to browsing than other noble broadleaved species, such as beech (*Fagus sylvatica*) and small leafed lime (*Tilia cordata).* When comparing with more common tree species in the Swedish landscape, e.g. Norway spruce (*Picea abies*) and silver birch (*Betula pendula),* oak is more preferred by herbivores (Gill 1992; Kullberg & Bergström 2001; Götmark et al. 2005). Sessile oak (*Quercus petrea*) has adapted to the high probability of browsing through redirecting resources, when browsed, to the roots. By creating well-developed root systems young oak seedlings become more resilient to browsing by giving them a higher chance of survival when their shoots are damaged (Drexhage & Colin 2003).

Oaks are generally considered as light demanding species that thrive in high light environments (Jensen et al. 2011; Sevillano et al. 2016). They are less competitive in shady environments compared to more shade tolerant tree species, such as beech or Norway spruce (Jensen and Löf 2017). Even though in the early stages of oak seedling establishment they are fairly resistant to competition, they have a difficulty to cope with such conditions over a longer period of time. Canopy openness is an important factor, as a more open canopy allows more available light to reach the forest floor and creates an environment where oak seedlings are given the opportunity to increase in size and vigour (Götmark 2007). Vigorous seedlings and saplings are more resilient to disturbance and therefore have a greater survival rate compared to the smaller plants grown in less open sites (Jensen & Löf 2017; Götmark 2007).

Also, the morphology of oak leaves is dependent on the light conditions. The leaves of oaks grown in high light conditions have a larger total mass compared to the leaves of oaks grown in low light conditions (Jensen et al. 2012b).

The aim of this study is to evaluate whether the light availability has an impact on browsing intensity as well as browsing frequency on naturally regenerated oak seedlings in different light treatments in southern Sweden. I hypothesise that browsing intensity and browsing frequency (predominantly caused by moose and roe deer) will be higher in the treatments with more light.

Material and method

Study sites

The study was conducted at five sites spread out in areas throughout southern Sweden (Fig. 1). Three of the sites are located within the ecopark Hornsö in the county of Kalmar. The ecopark is managed by Sveaskog and is mainly dominated by old Scots pine (*Pinus sylvestris*) forest. Within the dominating forest landscape of mixed coniferous forest, pasture areas, open landscape, and lakes are also present. In the plot areas pedunculate oak is the dominating species both in the overstorey and the ground vegetation. In addition to the dominating oak seedlings in the ground vegetation, billberry dwarf shrubs (*Vaccinium myrtillus*) also are present.

Site 4 is located in Sösdala, in the county of Skåne and surrounded by an agricultural landscape with patches of forest. There is a mixture of broadleaved tree species in the area, e.g. oak, beech and birch. In addition to the broadleaved dominated forest patches there are some coniferous stands dominated by Norway spruce. The plots dominant overstorey species is pedunculate oak, with a dominance of oak seedlings in the ground vegetation as well.

Site 5 is located close to the city Halmstad, in the county of Halland. The plots are located in a key habitat area dominated by oak in the overstorey. However, there is some ingrowth of Norway spruce as well. Around the area there is a mixed landscape of both production forest, composed of larch (*Larix spp.*) and Norway spruce, and agricultural fields.

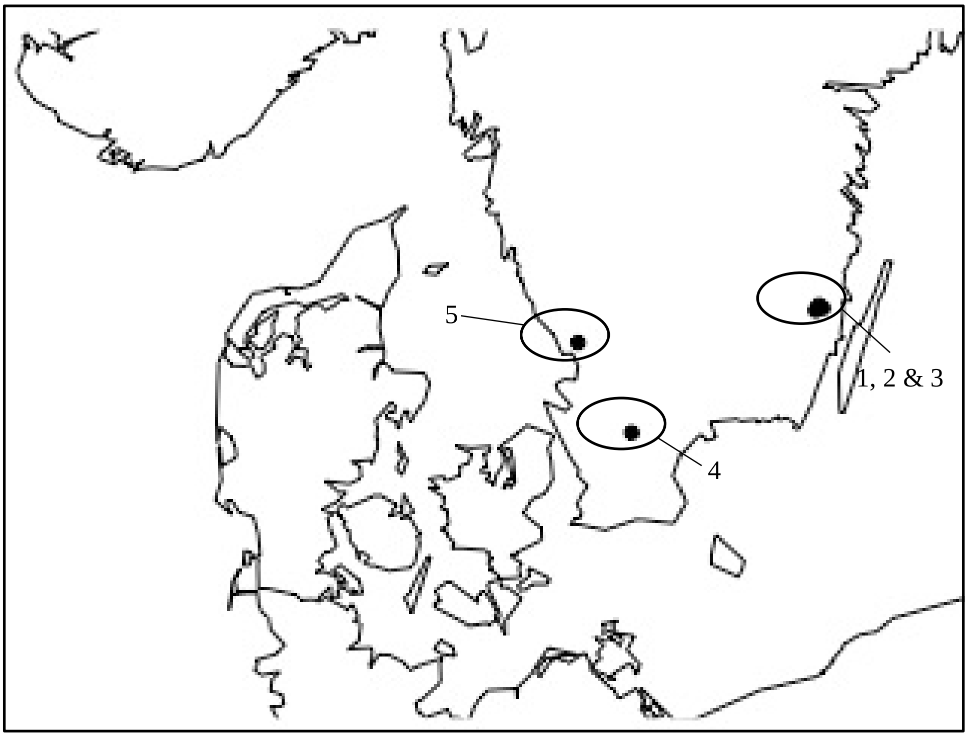

Figure 1. Map showing the locations of the five sample sites. Site 1, 2 and 3 are located in Hornsö, Kalmar, site 4 is located in Sösdala, Skåne, and site 5 is located in Halmstad, Halland. The map was created using the R-packages maps (Becker et al.2018a) and mapdata (Becker et al. 2018b)

Study design

At all the study sites, four 25 m^2 plots with naturally regenerated oak were marked in the spring of 2016. The plots were assigned two light treatments, low and high light, and one plot in each light treatment was fenced (Fig. 2). To create a high light environment in the treatment plots, canopy gaps of about 400 m^2 were created at each site with the two plots in its center. The two low light treatment plots remained underneath the closed forest canopy. Within the plots all naturally regenerated oak seedlings ≤200 cm in height, i.e. within browsing height, were marked with a unique tag for identification. A random selection of 38-68 seedlings per plot were chosen for measurements. These have been examined in inventories executed during spring and fall in 2016 and 2017, and spring in 2018. The plots used in this study were established as a part of a larger study setup by Linda Petersson in the spring of 2016.

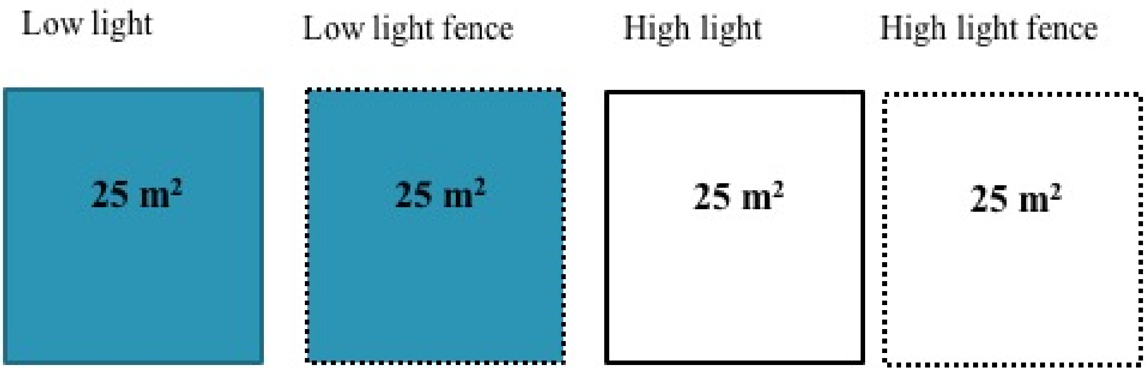

Figure 2. The experimental design with four 25m^2 treatment plots at one site: two in low light and two in high light environment. One fenced and one non-fenced plot in each light treatment.

Measurements

Measurements conducted between the spring of 2016 and the fall of 2017 were done by Linda Petersson. In the spring of 2018 all measurements at site 4 were made by both Linda Petersson and myself, and the remaining sites were measured only by me, Per Nordin.

Shoots

The number of primary shoots on every oak seedling chosen for measurements were counted at each inventory occasion. Primary shoots were defined as a shoot growing from the main stem (Fig. 3). Therefore, larger branches with multiple secondary shoots only count as one. Also, a primary shoot had to be more than 1 mm thick and 2 cm long. In order to examine the difference between the number of primary shoots in different light conditions an ANOVA was done.

Browsing damage

Browsing damages were recorded in a similar fashion as the number of primary shoots. The number of primary shoots that had been browsed within the time period since the last data gathering occasion were counted. When a shoot was dry the damage was determined to not be fresh and therefore not counted. If needed, to determine the freshness of a damage, the bark of the shoot was scraped lightly. If several secondary shoots on a branch were browsed it still counted as one damage (Fig. 3). When a browsing damage was recorded, the browsing species and browsing class were also noted. Species accounted for were hare and cervids, no distinction were made between moose, roe deer, fallow deer, or red deer. Moose and roe deer are the most common cervid browsers in the study area. Rooting damage from wild boar was observed but not included in the study. Browsing class involves which shoots that had been browsed, either only the terminal shoot, only lateral shoots, or both terminal and lateral shoots (Fig. 3).

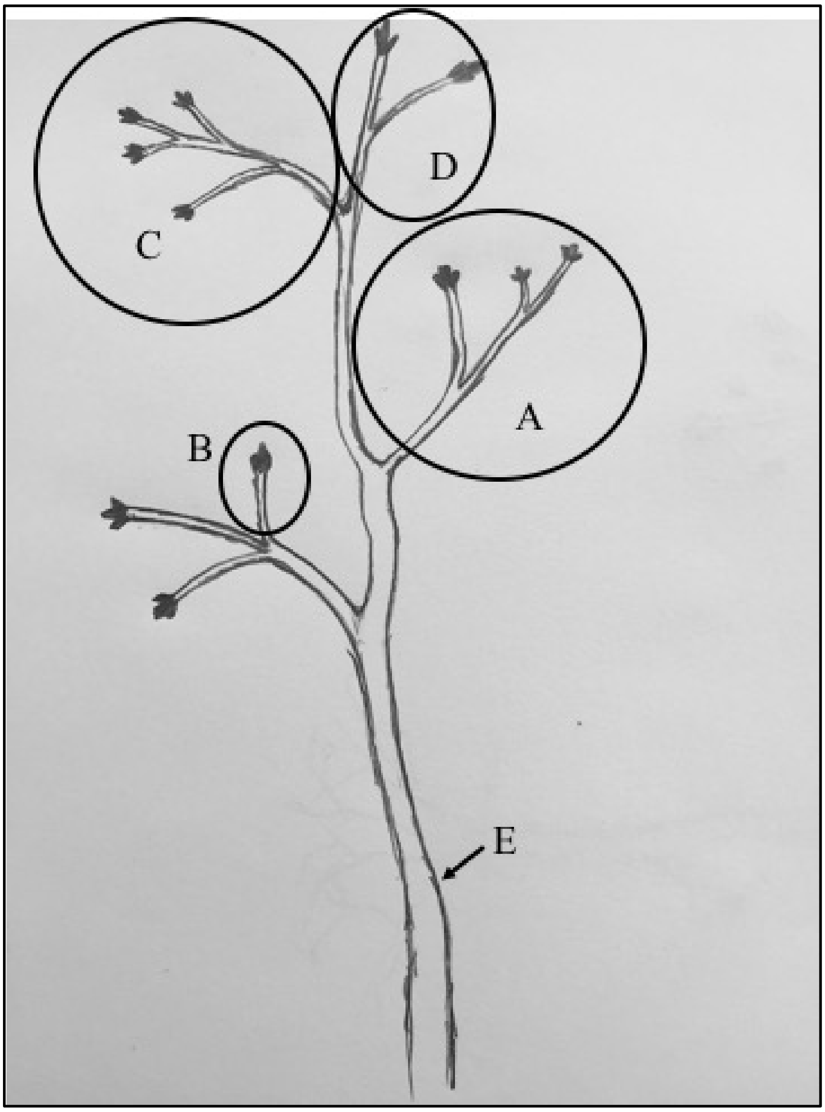

Figure 3. An illustration of an oak seedling. A = Primary shoot, B = Secondary shoot, C = Lateral shoot, D = Terminal shoot, E = Main stem.

Height and relative height growth

Oak seedling height (±1 cm) used in this study was measured in the spring of 2016 and fall of 2017 by Linda Petersson (Appendix I). From these heights the relative height growth was calculated using a formula (Fig 4). Then the mean relative height growth for each site and treatment was calculated. To determine whether there was a difference in relative height growth between treatments three different ANOVAs were conducted. One including data for all plots, one with data from only fenced plots, and one with data from only non-fenced plots.

$$\frac{Log(Height\ Fall\ 2017) - Log(Height\ Spring\ 2016)}{Years}$$

Figure 4. The formula used to calculate relative height growth for individual seedlings.

Light

To measure the amount of light transmitted down to the forest floor fisheye photographs were used. Photographs were taken during overcast days in summer when all trees have leaves using a Nikon Coolpix 880 VR digital camera with a LC-ER2 fisheye lens. To analyze these fisheye photos a program called Gap Light Analyzer, GLA, was used. This program is able to analyze the percentage of above canopy radiation that reaches the camera lens underneath the canopy (Frazer et al. 1999). All light data used in this study was measured in 2016 and 2017 by Linda Petersson. No light measurements had yet been done in 2018, therefore the light data from 2017 was used for 2018 as well. An ANOVA was conducted to investigate the difference in light availability between light treatments.

Fecal pellet count

To get an overview of the intensity of usage of cervids in the study sites a fecal pellet count was conducted. Twenty sample plots were placed in a quadratic grid 200 meters apart surrounding the light treatments plots, creating a transect area of 1x1 km (Fig. 5). All the sampling plots were in forest land and if placed on non-forested land the plot was moved. The plots are of circular shape and varied in size depending on the species the droppings come from (Fig. 6). For moose the plot area was 100 m^2, and for deer (roe deer, red deer, and fallow deer) the plot area was 10 m^2. Only piles larger than 20 pellets were counted. When such a pile was found it was removed from the plot to avoid it to be counted at the next sampling occasion. To calculate an index of density for each site and gathering occasion, the number of piles from moose and the three deer species were combined and then divided by the number of sample plots.

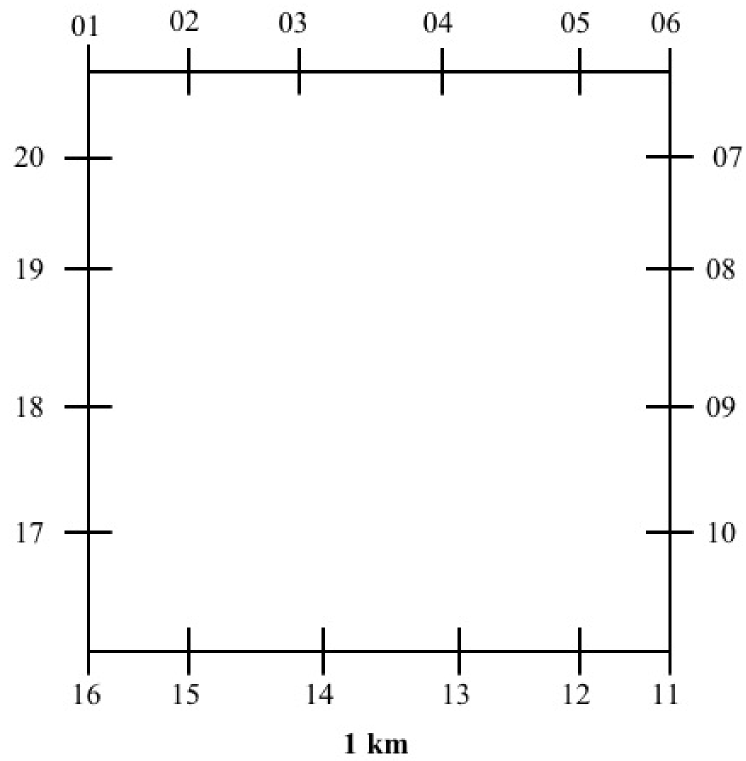

Figure 5. Twenty circular plots placed in a quadratic grid 200 m apart. The transect area is 1x1 km with the light treatment plots located in the center.

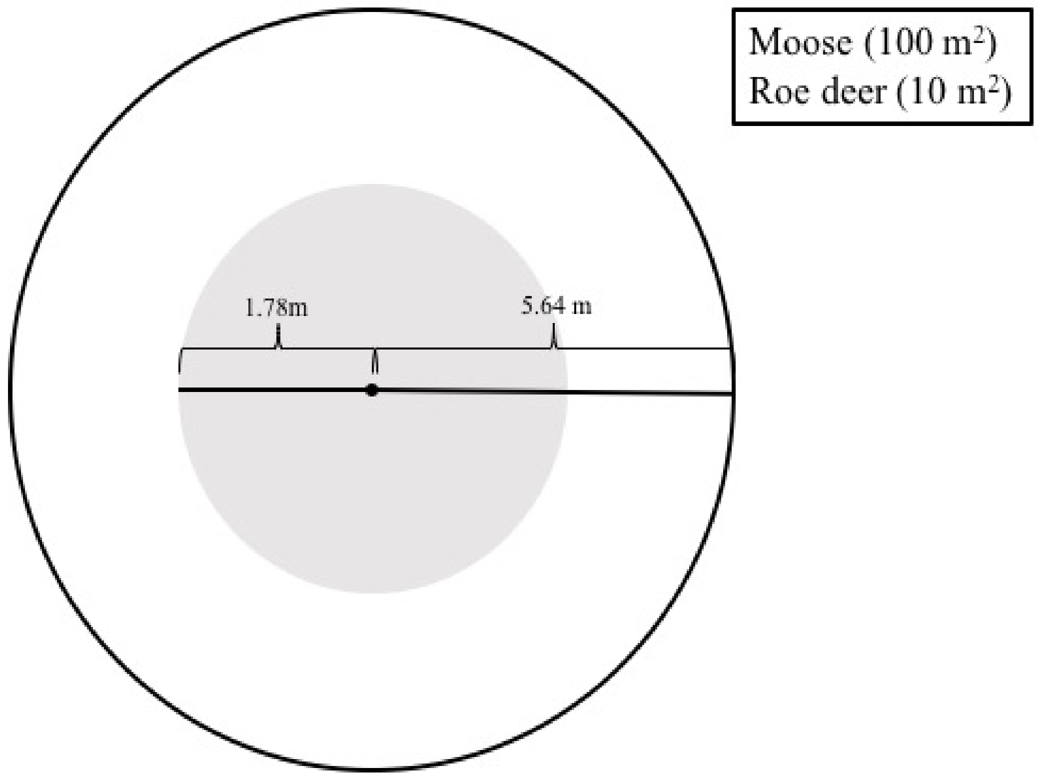

Figure 6. Circular plot design used in the fecal pellet count. The grey circle represents the 10 m^2 area used for roe deer, red deer and fallow deer, and the white circle represents the 100 m^2 area used for moose.

Statistical analysis

All the statistical analyses in this study were done using R-version 3.4.3 (R-core Team 2017). To determine initial differences in browsing frequency and browsing intensity with different light availability an ANOVA was conducted. Two linear mixed regression models, using the R package lme4 (Bates et al. 2015), were used in the statistical analysis. Variables used in the model were divided between dependent, independent, and random variables. The dependent variables were cervid browsing intensity and browsing frequency. Browsing intensity was calculated as the number of browsed shoots divided by the total number of shoots of an individual seedling. Thereafter, the mean browsing intensity was calculated for each site, inventory occasion (time) and light treatment. Browsing frequency was calculated as the number of browsed seedlings divided by the total number of seedlings within a plot. Mean values were then calculated for each site, inventory occasion (time) and light treatment. The independent variables for both models were *light*, *total number of oaks* and *time*. Light was represented by a mean value from the fisheye photographs for site and time, total number of oaks was the number of oak seedlings within a single plot, and time was the season when the data was gathered. To cope with variation between the study sites a random factor *site* was included in both models. Only data from the non-fenced plots were used in the analysis. Since the linear mixed regression function in lme4 (Bates et al. 2015) did not generate any p-values, a likelihood ratio test was conducted. The test compared models with or without the independent variable of interest resulting in a p-value that represented the significance of that independent variable.

Results

Light

Available light did differ significantly between the light treatments in 2016 (p <0.001), though variation in light availability was greater in the high light treatment where gaps were created (Fig. 7). There was also a variation in light availability between sites in the high light treatment (Fig 8). Light availability was lower in site two and three and higher in site one and five.

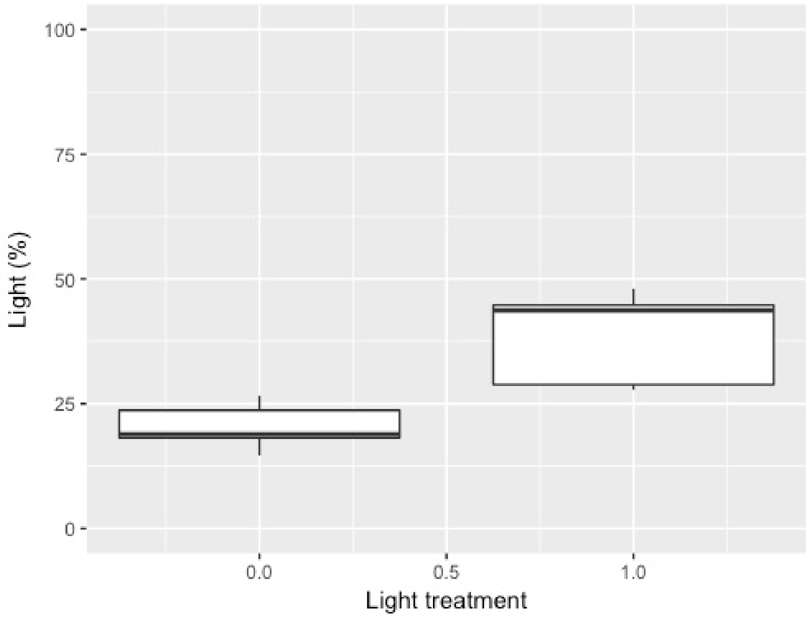

Figure 7. The difference in light availability between the two light treatments based on fisheye photographs in 2016. 0 = Low light treatment, 1 = High light treatment.

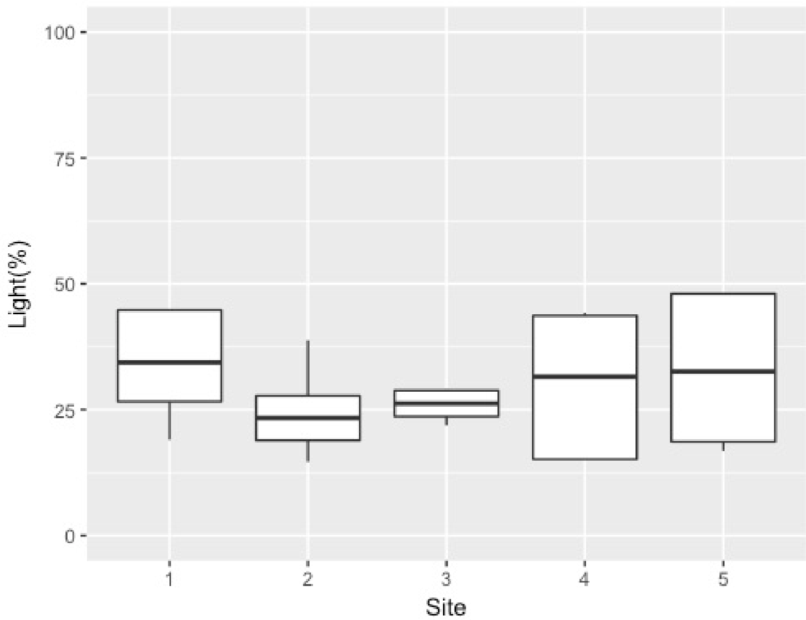

Figure 8. The difference in light availability in the high light treatment between the five study sites based on fisheye photographs in 2016.

Relative height growth

The relative height growth of oak seedlings did differ depending on the light availability created in the two light treatments. The overall ANOVA-test, including both fenced and non-fenced plots, was not significant ($p = 0.077$) (Fig. 9A). In the fenced plots the variance was greater than in the non-fenced plots but did not show a significant difference between light treatments ($p = 0.286$) (Fig. 9B). In the non-fenced plots, the relative height growth was significantly different between light treatments ($p = 0.045$) (Fig. 9C).

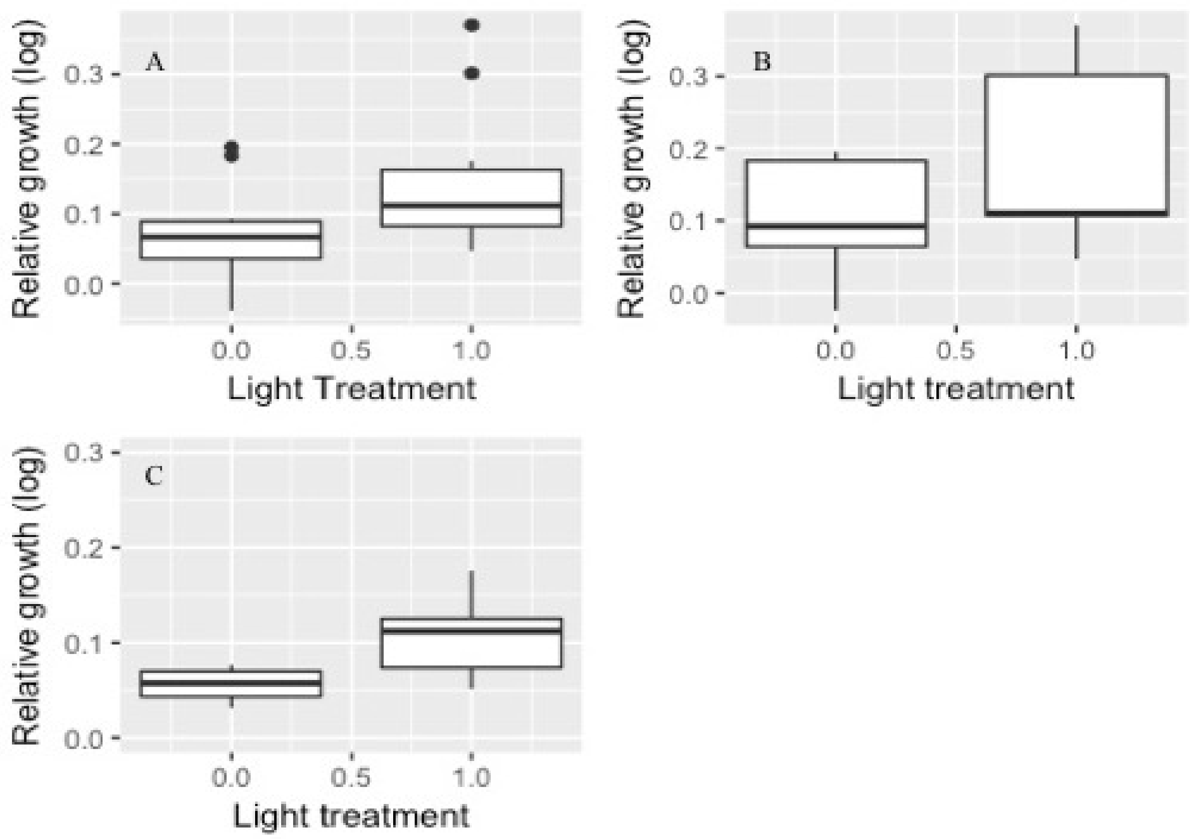

Figure 9. Boxplots showing the difference in relative height growth of oak seedlings between the spring of 2016 and the fall of 2017 in the two light treatments with or without fencing. 0 = Low light, 1 = High light. A = All seedlings, B = Fenced plots, C = Non-fenced plots.

Total number of oak seedlings

The total number of oak seedlings varied among the study sites and the two light treatments (Table 1). In comparisons to the other areas examined, site 4 had a lower number of sampled oaks with below 50 in both light treatments. The other sites showed variation among each other, with the largest number of oak seedlings in the low light treatment in site 3 (214 oak seedlings).

Table 1. Table showing the total number of oaks seedlings per site and light treatment and the number of measured oak seedlings per site and light treatment.

	Treatment		Measured oak seedlings	
Study site	**Low light**	**High light**	**Low light**	**High light**
Site 1	186	161	56	62
Site 2	115	73	58	61
Site 3	214	130	54	67
Site 4	38	49	26	44
Site 5	175	152	43	45

Number of primary shoots

The mean number of primary shoots per oak seedling was different between light treatments and between time of sampling (Table 2). In plots with high light levels, oak seedlings had a higher mean number of primary shoots compared to the seedlings in plots with low light levels (Table 2). The differences were statistically significant between low light and high light ($p < 0.001$).

Table 2. The mean number of primary shoots per oak seedlings for the two light treatments at the four sampling occasions.

	Treatment	
Time	**Low light**	**High light**
Fall 2016	5.23	5.24
Spring 2017	4.89	5.34
Fall 2017	5.38	6.33
Spring 2018	5.31	6.12

Browsing species

In this study, the recorded browsing damage by cervids (mainly moose and roe deer) was by far the greatest in numbers. Compared to damage by both hares and rodents, damage by cervids was more common (Table 3). Therefore, damage by hares, rodents, and unknowns were excluded from the mixed regression analysis.

Table 3. Table showing the number of recorded browsing damage per species. Cervids include moose, roe deer, fallow deer, and red deer. Rodents include voles and mice. A damaged plant could be counted twice if browsed by multiple species.

Species	**Recorded browsing**
Cervids	343
Hare	36
Rodent	1
Unknown	1

Relative habitat use by cervids

Relative habitat use by cervids, as indexed by the fecal pellet count, was different between years and sites. The trend showed that cervids were using sites more intensely in spring time compared to fall. Generally, the sites in Hornsö (Sites 1, 2 and 3) were more intensely used by cervids compared to the other two sites, with an exception for the spring of 2018. The site in Halmstad, site 5, was the least intensely used site at all sampling occasions (Fig. 10).

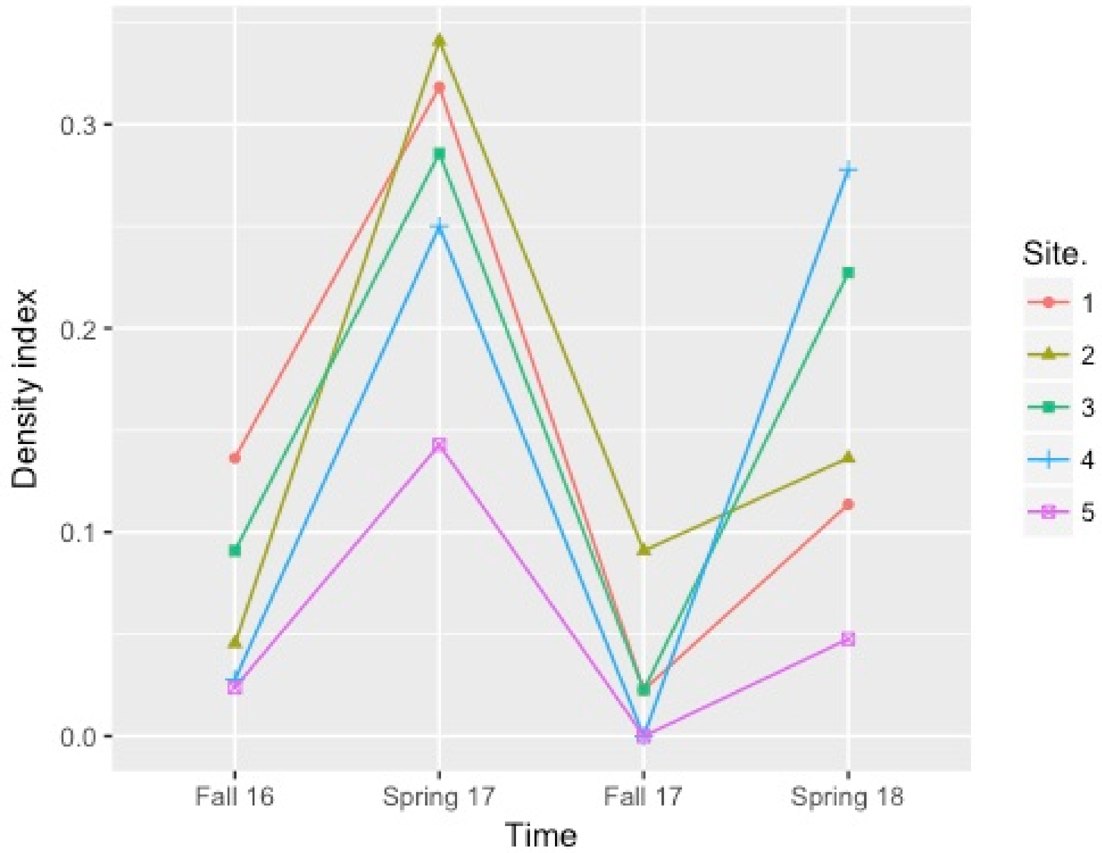

Figure 10. Graph showing the density index of droppings from the four cervid species (moose, roe deer, red deer, and fallow deer) in the five sites from the four sampling occasions.

Initial browsing frequency and intensity

Browsing intensity (the proportion of browsed shoots per individual seedling) and browsing frequency (the proportion of browsed seedlings) did not differ significantly between the two light treatments when the plots were established in 2016 (browsing intensity $p = 0.792$ and browsing frequency $p = 0.754$) (Fig. 11). When differentiating the five sites, variance can be seen in both browsing frequency and browsing intensity (Fig. 12).

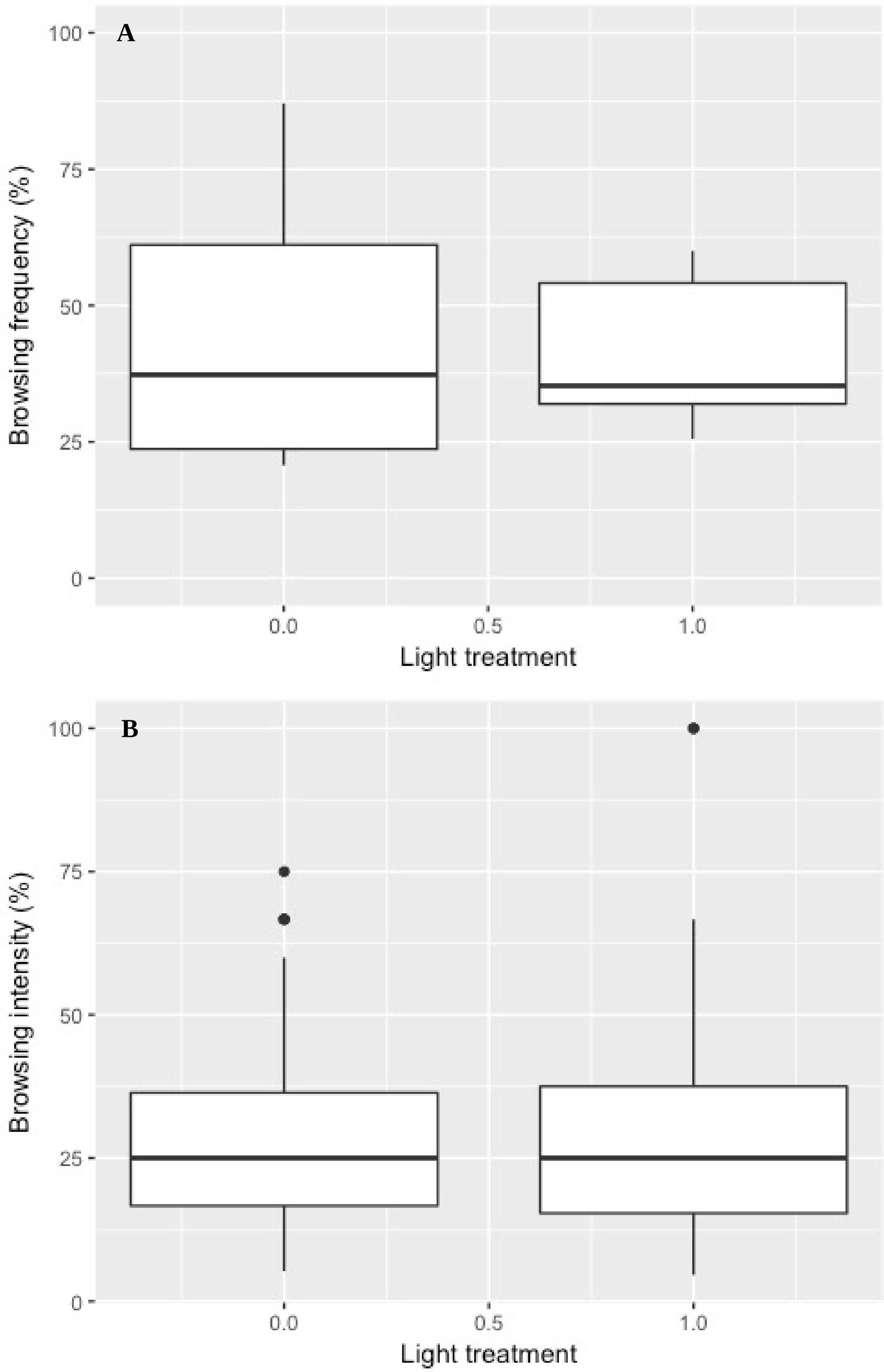

Figure 11. Boxplots showing initial A=browsing frequency and B=browsing intensity in the spring of 2016 for the two light treatments. 0 = Low light treatment, 1=High light treatment.

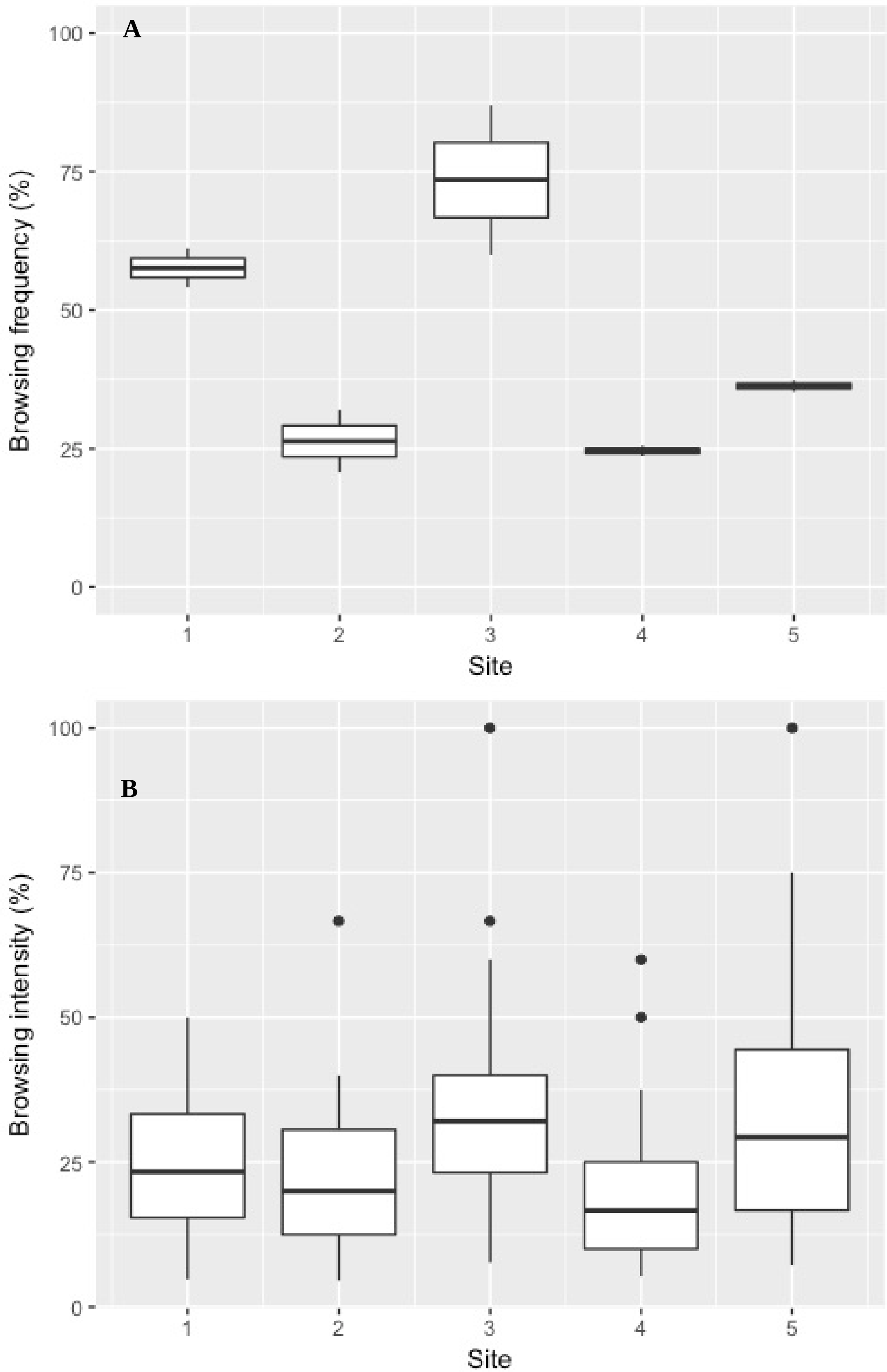

Figure 12. Boxplots showing the initial A=browsing frequency and B=browsing intensity in the spring of 2016 for the five study sites in southern Sweden.

Browsing intensity and frequency

The linear mixed regression analysis showed that light did not have a statistical significant effect on neither cervid browsing intensity (p = 0.1185) nor browsing frequency (p = 0.3818) (Table 4). When reanalysing the data using only spring data, browsing intensity was affected. The level of significance changed and showed a p-value closer to 0.05 although still not statistically significant (Table 5).

In the models used to analyse cervid browsing data, the independent value of *Time* showed to be important. Time had a statistically significant effect on browsing intensity (p = 0.0016) and on browsing frequency (p <0.001) (Table 4). Spring had a positive effect on browsing frequency (Fig. 13), meaning that a larger number of oaks were affected by browsing in spring time compared to fall. Time also showed a significant effect on browsing intensity, though not as strong effect as on browsing frequency (Fig. 14).

Table 4. The output of the mixed regression analysis with data from all gathering occasions. P-value for time is estimated for whole factor but the estimates are for the different levels within time.

		Browsing intensity			**Browsing frequency**	
Variables	**Estimate**	**Std. Error**	**p-value**	**Estimate**	**Std. Error**	**p-value**
Light	-0.0027	0.0017	0.1185	0.0012	0.0013	0.3818
Time			0.0016			<0.001
Fall 2016	0.4215	0.1029		-0.0674	0.0700	
Spring 2017	0.0638	0.0735		0.2970	0.0410	
Fall 2017	-0.1939	0.0858		0.0091	0.0410	
Spring 2018	-0.0708	0.0736		0.2563	0.0410	
Total Oaks	0.0005	0.0004	0.2032	0.0004	0.0004	0.3626

Table 5. The output of the mixed regression analysis with only spring data.

		Browsing intensity			**Browsing frequency**	
Variables	**Estimate**	**Std. Error**	**p-value**	**Estimate**	**Std. Error**	**p-value**
Light	-0.0033	0.0018	0.0780	0.0012	0.0023	0.5987
Total Oaks	0.0004	0.0004	0.2592	0.0005	0.0006	0.5113

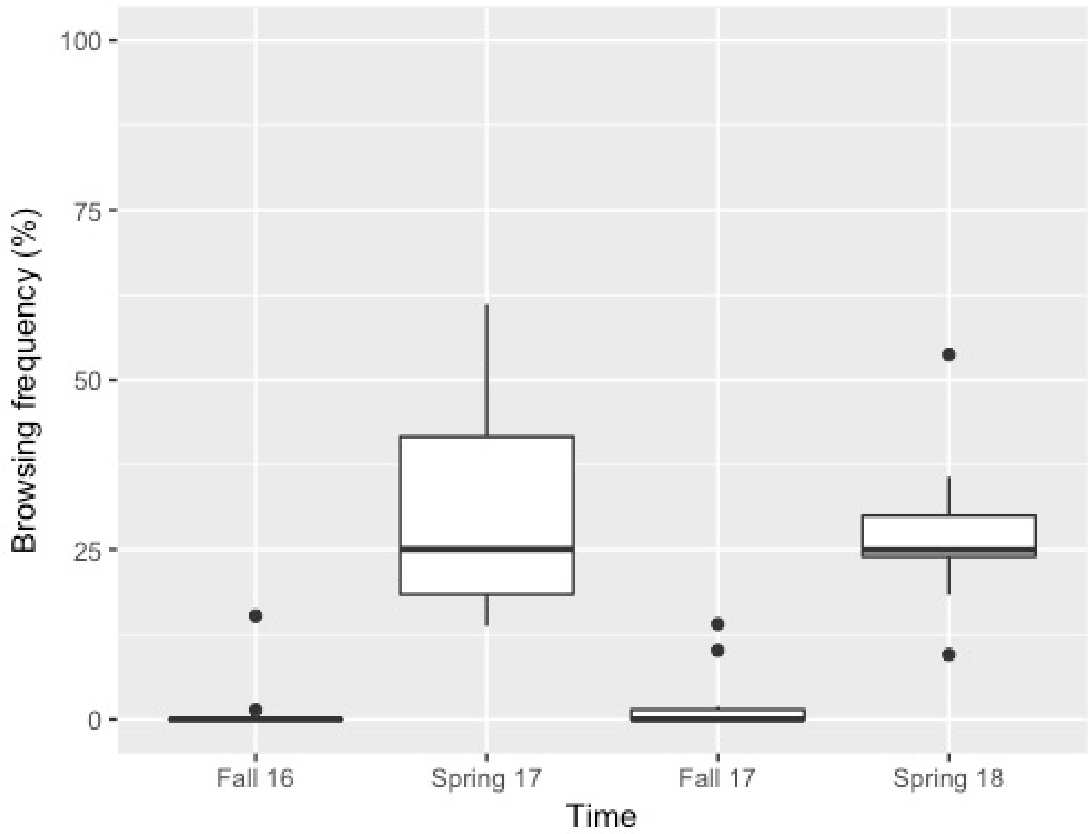

Figure 13. Browsing frequency dependent on time.

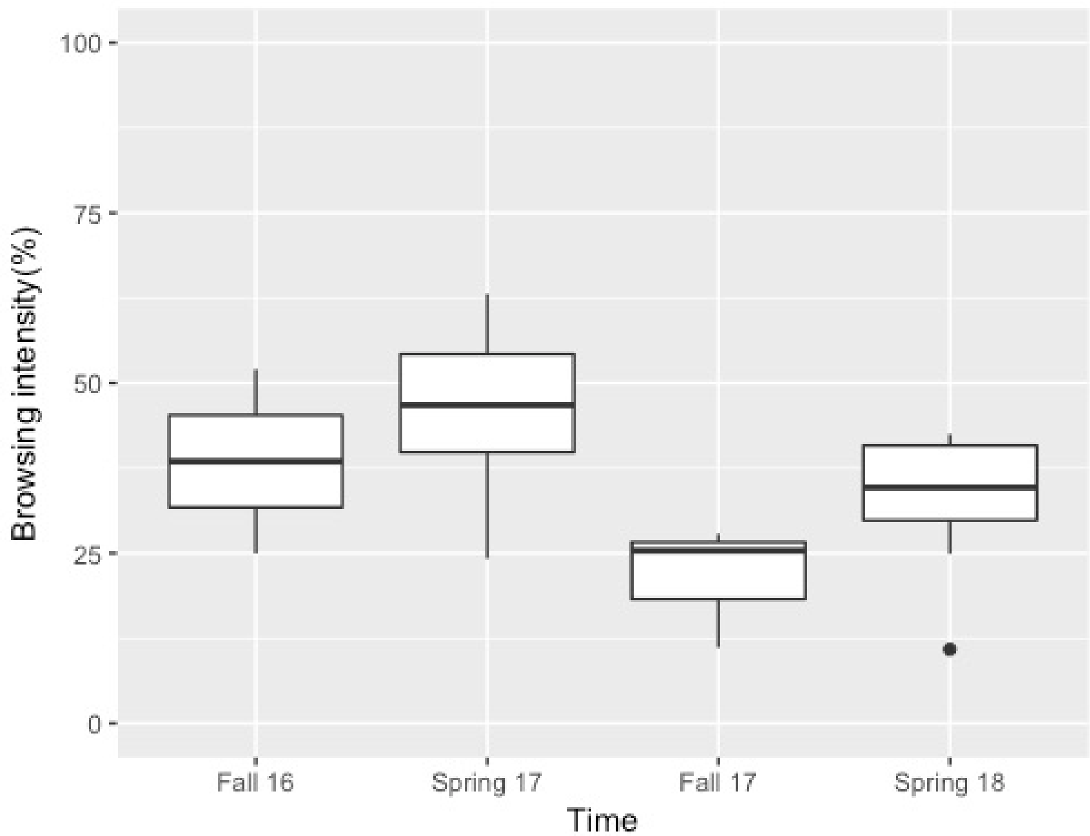

Figure 14. Browsing intensity dependent on the time.

Discussion

Influence of light on browsing intensity and frequency

The hypothesis behind this study was that increased light availability would lead to an increased browsing intensity and an increased browsing frequency on naturally regenerated oak seedlings. The result, however, showed that there was no statistically significant effect of increased light on neither browsing intensity nor frequency. A similar result has been found in another study examining the relationship between light and browsing intensity in silver fir, where light did not show a significant effect on browsing intensity (Kupferschmid et al. 2013). Furthermore, browsing frequency by white tailed deer (*Odocoileus virginianus*) was shown to be unaffected by harvesting measures, which created different light conditions, according to a study on white oak (*Quercus alba*) and black oak (*Quercus velutina*) (Kellner and Swihart 2017).

In contrary to these findings, Churski et al. (2017) showed that a number of European temperate broadleaved species were more likely to be browsed when growing in high light, including pedunculate oak. Kuijper et al. (2009) also found a positive relationship between cervids feeding behaviour and increased light. These two studies, however, were conducted in the Bialowieza forest in Poland, an area with larger proportions of palatable species such as oak. My study on the other hand was conducted in areas not overall dominated by broadleaves. The study areas were instead dominated by conifers, which are less preferred by browsers (Gill 1992). Therefore, one could argue that the results of this study are indicators of relative selectivity and resource usage of herbivores, i.e. that subtle differences in the quality of neighbouring plants of the same species is of less importance when there is low abundance of palatable species in the landscape in relation to the number of cervids.

Other studies have shown that presence of more palatable species in an area can lower the overall browsing frequency on oak (Götmark et al. 2005). The relative selectivity of food sources by cervids is influenced by multiple factors that make the topic highly complex. Light, as examined in this study, influences nutritional content in plant species. Orchardgrass (*Dactylis glomerata*) in the eastern U.S. has shown to contain different nutritional content depending on light availability (Belesky et al. 2006). However, these differences in nutritional values are not necessarily better or worse but simply good from different point of views depending of which nutrients that are of importance for the individual cervid. This highlights the complexity of what cervids choose to forage and may not be determined by a single factor, such as light, but is also influenced by other micro site factors such as soil fertility (Ball et al. 2000).

The importance of season

Time of year showed to be a significant factor for both browsing intensity and browsing frequency on naturally regenerated oak seedlings, as data gathered in spring-time showed a greater browsing frequency than data gathered in fall-time. These results show that browsing frequency on oak shoots was higher in winter and early spring, compared to summer and early fall. An explanation for these results could be the seasonality in cervid foraging behaviour. In winter many food sources, such as forbs and grasses, are less available which make alternative food sources, such as tree shoots and twigs, more important (Kullberg & Bergström 2001; Palmer et al. 2004; Moser et al. 2006).

The diet of cervids has been shown to change depending on the season, being more dependent on trees as a food source during winter, resulting in an increased browsing frequency on oak seedlings this time of year (Palmer et al. 2004; Gill 1992). However, dietary choices differ between deer species and populations. Moore et al. (2000) showed that browsing frequency on oak was higher in summer when examining browsing by fallow deer in Great Britain. Roe deer shows a pattern of increased browsing when other resources in winter are sparse (Tixier & Duncan 1996). Red deer feeds on oak all year around just as many other deer species, but increasingly so in winter (Palmer et al. 2004).

Habitat selection could also explain the increased browsing frequency in winter and early spring. In North America, white tailed deer choses habitat based on forage availability and abundance, and they changed their ranging behavior depending on season (Massé & Côté 2012). Since the diet of roe deer often consists of items found in the agricultural fields (Tixier & Duncan 1996), areas with a high abundance of food, one could argue that there is a similar pattern for roe deer as for white tailed deer in North America. It is therefore likely that roe deer choses to feed more in the agricultural fields surrounding some of the study sites during the growing season and more in the forested areas during winter. This is further supported by the differences in density of droppings that were consistently higher during the spring inventories at all of the study sites, indicating a higher usage of forested areas during winter.

Comparing browsing frequency from this study with inventories done by The Swedish Forest Agency through *Äbin* (https://www.skogsstyrelsen.se/abin (*access 13/6-2018*)), shows that the browsing frequency is high in all of the study sites on the landscape level as well, not just within the plots. In this study, the density of droppings was the lowest in the site in Halmstad, Halland, at all of the inventory occasions, which could be explained by the overall tree species composition in the young forest on the landscape level. Tree species composition around the site in Halmstad, Halland (site 5) is less diverse than the sites in Hornsö, Kalmar (site 1, 2 and 3) (Skogsstyrelsen 2018a; 2018b). *Äbin* only includes young forest and browsing damages to the leader shoots on the main crop trees Scots pine and Norway spruce, but even so it can still indicate the relative intensity of usage by cervid browsers on a larger landscape level. However, one should consider the importance of other forest types in the landscape as well when evaluating moose feeding behaviour (Bergqvist et al. 2018).

Further considerations

In future studies of browsing intensity in different growing conditions, one should consider how to calculate browsing intensity. In this study, browsing intensity was calculated by dividing the number of browsed shoots by the total number of shoots on the individual seedling. However, seedlings grown in high light conditions will have a higher number of shoots compared to seedlings grown in low light conditions (Ziegenhagen & Kausch 1995;

Jensen et al. 2012b; Sevillano et al. 2016). This relationship between light and number of shoots leads to difficulties when interpreting proportions of browsed shoots. Proportions of browsed shoots will be lower in high light even though the same number of shoots have been browsed as in low light because of the difference in the total number of shoots in the two light environments.

On a landscape scale, future studies should examine the selectivity of browsers based on food quality in relation to per-capita availability. In a landscape with low variability and low amount of palatable tree species per individual animal, intra-specific selectivity among such plant individuals may be harder to detect. Studies in areas with high abundance of highly palatable food resources are needed to investigate if there is a strong selectivity of food quality by browsers.

Conclusion

Light had no significant effect on cervid browsing intensity or browsing frequency on naturally regenerated oak seedlings. Landscape level factors may have influenced this lack of selectivity on food quality, as overall selectivity for oak seedlings may have been increased by the lack of other palatable species in the landscape. Time of year significantly influenced both the browsing frequency and intensity, with a higher browsing frequency on oak seedlings in winter and early spring compared to summer and early fall. Habitat selectivity and use intensity was influenced by time showing that the areas in this study was used more intensely during winter and early spring than summer and early fall. In conclusion, this study showed that cervids chose to browse on oak seedlings differently depending on the time of year and that there was no effect from the light conditions the oak seedlings were growing in. Further studies are needed to determine the relationship between food abundance and food quality selectivity.

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Appendix I. Oak seedling size distribution in 2017