

Summer and winter browsing affect conifer growth differently: An experimental study in a multi-species ungulate community

Sabine E. Pfeffer^{a,*}, Navinder J. Singh^a, Joris P.G.M. Cromsigt^{a,b,c}, Fredrik Widemo^a

^a Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

^b Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, 6031 Port Elizabeth, South Africa

^c Copernicus Institute of Sustainable Development, Utrecht University, 3584CS Utrecht, the Netherlands

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ABSTRACT

Ungulate browsing has been studied for several decades in the northern hemisphere. However, studies have mainly focused on just one or two ungulate species, while rarely contrasting the relative effects of summer and winter browsing. This limits our understanding of the dynamics and effects of browsing in landscapes where ungulate species diversity is increasing. We conducted a seasonal exclosure experiment on former clear-cuts in a multi-species ungulate system in Sweden, to investigate the relative impacts of summer and winter browsing on the conifers Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) at the tree species level. We tested for differences in individual conifer growth and demographic responses between *Summer browsing*, *Winter browsing*, *No browsing*, and *Control* treatment plots over a 4.5 year experimental period. We defined the demographic response as the distribution of conifers among different height classes. Individual growth rates and demographic responses of both conifer species were similar in the plots with *No browsing* (year-round exclosures) as in the *Control* plots with year-round browsing. Plots subject to *Summer* and *Winter browsing* differed in terms of their demographic response relative to plots with *No browsing* and *Control* plots; more stems reached taller height classes in the *Summer* and *Winter browsing* plots with slight differences between the conifer species. We discuss the different responses of Scots pine and Norway spruce considering their differences in palatability and their ability to tolerate plant-plant competition in a multi-species ungulate system, in light of potential associational effects. If fencing is intended to be used as a management practice to mitigate the impacts of deer browsing on conifer growth, our results suggest that a total exclusion of deer does not necessarily enhance conifer growth during the first years of regeneration.

1. Introduction

The impacts of ungulate browsing in the northern hemisphere have been studied for decades. A major focus on this work has been on the impact of browsing in the light of ungulate-forestry interactions (Reimoser and Putman, 2011). The majority of these studies looked at the direct impact of winter browsing and environmental variables predicting winter browsing (e.g. Ball and Dahlgren, 2002; Bergqvist et al., 2014; Danell et al., 1991; Kullberg and Bergström, 2001; Milligan and Koricheva, 2013; Zhong et al., 2020). Although ungulates browse during summer as well, much fewer studies investigated the effects and drivers of summer browsing (e.g. Bergström and Danell, 1995; Bergqvist et al., 2013; Nichols and Spong, 2014). Moreover, studies contrasting summer and winter browsing are rare (e.g., Danell et al., 1994; den Herder et al.,

2009). The limited number of studies on the relative effects of summer and winter browsing on plant species and ecosystems limits the understanding and knowledge on which actions to manage ungulate-forestry interactions are based.

Ungulate browsing affects plant communities directly but also indirectly (Rooney and Waller, 2003). Winter browsing affects tree growth mostly in a direct way through the removal of shoots, browsing on the apical leader shoot, and stem breakage (Danell et al., 1994; Bergqvist et al., 2014), mainly resulting in reduced tree height and wood quality especially for conifers (Danell et al., 2003; Bergqvist et al., 2014). Summer browsing affects tree growth and recruitment directly but often also indirectly, especially when focusing on the recruitment of conifers. Summer browsing predominately focuses on deciduous trees (Bergström and Danell, 1995), where leaf stripping of deciduous trees during

* Corresponding author.

E-mail address: sabine.e.pfeffer@gmail.com (S.E. Pfeffer).

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summer may directly affect their photosynthetic activity and shoot sizes, but also budburst during the following vegetation season (Danell et al., 1994; den Herder et al., 2009), both potentially reducing tree growth. Reduced growth of deciduous trees due to browsing may, indirectly, positively affect the growth of conifer species by reducing plant-plant-competition between deciduous and conifer species (Kuijper et al., 2010; Stokely and Betts, 2020; Vuorinen et al., 2020).

Tree responses to summer and winter browsing differ due to induced morphological and physiological changes. Moreover, the effects of summer and winter browsing on plant growth and morphology can be either opposing or additive (Danell et al., 1994; den Herder et al., 2009). For instance, trees have been observed to respond to shoot removal during winter with an increased shoot growth, whereas shoot removal during summer may have the opposite effect (Danell et al., 1994). However, tree responses to both summer and winter browsing are often only visible during the following growing season, where plants respond quantitatively but also qualitatively (den Herder et al., 2009). Thus, both summer and winter browsing can lead to changes in forage availability. In multi-species ungulate communities, the relative effects of winter and summer browsing become germane since ungulate species differ in their seasonal use of tree species and their diet similarity changes throughout seasons with higher dietary overlap during winter than summer especially in Nordic environments (Spitzer et al., 2020). Thus, different impacts of summer and winter browsing can be expected on forest production in varying seasons. Furthermore, browsing impacts on the plant community can change in landscapes where multiple co-occurring ungulate species interact (Latham, 1999; Young et al., 2005).

We are not aware of any studies that specifically contrasted the impacts of summer and winter browsing in a multi-species ungulate system (but see Danell et al. (1994) and den Herder et al. (2009) for studies on moose). Moreover, our current understanding of the impacts of summer versus winter browsing is largely based on observational studies, while evidence from experimental studies is limited (Milligan and Koricheva, 2013). Most experimental browsing studies compared only the effects of year-round browsing exclusion with a control (e.g., Speed et al., 2013; Bloodworth et al., 2020; Vuorinen et al., 2020). Additionally, manipulated factors such as management practices have been studied in an experimental enclosure setup (e.g., herbicide control: Stokely and Betts, 2020; fire intensity: Petersson et al., 2020) but without contrasting summer and winter browsing.

Here, we present the results of a replicated field experiment with seasonal enclosures to specifically separate the effects of summer and winter browsing on the conifer growth of economically important Scots pine (*Pinus sylvestris*, hereafter pine) and Norway spruce (*Picea abies*, hereafter spruce) in regenerating clear-cuts. We compared the effects of *Summer browsing* (winter exclusion), *Winter browsing* (summer exclusion), *No browsing* (year-round exclusion) and *Control* (year-round browsing) plots in a Swedish multi-species ungulate system composed of moose (*Alces alces*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). These ungulates may control recruitment of trees into taller size classes via direct top-down effects (Kuijper et al., 2010). Such direct control of recruitment into taller size classes is also known as demographic bottleneck (Churski et al., 2017). We thus measured recruitment as (i) growth responses of individually marked conifers and (ii) demographic responses (i.e., the number of conifer stems in different height classes) during a 4.5 year experimental period. Due to varying palatability of the two conifer species, we expected summer and winter browsing to affect their growth responses differently. Pine recruitment should be more susceptible to ungulate herbivory than spruce (Speed et al., 2013; Vuorinen et al., 2020). Additionally, we expected different overall growth responses between the *Summer* and *Winter browsing* plots both through the direct effects of browsing (den Herder et al., 2004; den Herder et al., 2009) and through indirect effects from reduced plant-plant-competition due to browsing of deciduous species (McLaren et al., 2009). Thus, we also analyzed how summer and winter browsing

affected densities of deciduous trees and how deciduous competition may impact conifer tree growth. We discuss our results based on potential plant-plant-competition effects and the theory of associational effects due to differences in palatability.

2. Material and methods

2.1. Study area

We performed a replicated enclosure experiment in the eastern part of Södermanland county, Sweden (58.9° N, 17.1° E; Fig. 1), which is located in the hemi-boreal vegetation zone (Ahti et al., 1968). During the study period (Oct 2015 – April 2020), the study area (~440 km²) had a mean daily temperature of 7.4 °C and a mean daily precipitation of 1.4 mm (SMHI, 2020). The terrestrial landscape of the study area is dominated by coniferous forest (22% pine forest, 10% spruce forest, 10% mixed coniferous forest), arable land (16%), and re-growing areas with trees < 5 m (8%; i.e., clear-felled, storm-felled or burnt; Naturvårdsverket, 2019). Five wild ungulate species co-occur in the study area; moose, red deer, fallow deer, roe deer, and wild boar. Based on dung pellet group counts in the overall study area, mean (±SD) density indices during winter (2015/16–2019/20) for each species respectively are 0.15 (±0.18), 0.10 (±0.17), 4.51 (±4.61), 1.12 (±1.76), and 0.74 (±1.69) pellet groups per 100 m² (see Appendix A.1 for details on the sampling regime and the extraction of density indices represented by dung counts).

2.2. Experimental setup

We replicated four browsing treatments at ten sites across the study area: no browsing (year-round exclusion), summer browsing only (exclusion during winter), winter browsing only (exclusion during summer) and year-round browsing (no exclusion, i.e. control; Fig. 1). Each site was a former clear-cut (approx. 1.5–6.5 ha) that had been subjected to scarification prior to regeneration. One of the ten sites was clear-cut in 2013 and naturally regenerated with pine using seedling trees, whereas all other nine sites were clear-cut in 2014. In 2015, one of these nine sites was planted with pine and eight sites were planted with spruce of which two also had seedling trees of pine. Thus, pine and spruce are considered as the production trees in this study. Conifers were approx. 20 cm tall when planted.

In October 2015, we created four 14 × 14 m plots in each site (Fig. 1). The placement of plots was randomized within each site, while making sure that plots had a minimum distance of 28 m (2x 14 m) to each other and also to the edge of the clear-cut. Patches with unproductive forest land, exposed bedrock, large boulders, or mires were avoided within sites. Among the four plots per site, we randomly assigned the above-mentioned browsing treatments: permanently fenced (hereafter, *No browsing*), fenced during the growing season (April–September) but unfenced during the rest of the year (hereafter, *Winter browsing*), fenced during the dormant season (October–March) but unfenced during the rest of the year (hereafter, *Summer browsing*), and unfenced year-round (hereafter, *Control*; Fig. 1). For each plot, including the *Control*, we erected 16 wooden posts in a quadrat (Fig. 1); in some cases placement had to be slightly adjusted as hidden bedrock prevented erecting the posts. When fenced, 16 metal frames each 3.5 × 2 m were attached to the posts using cable ties. The mesh size was 10 × 26 cm, such that ungulates were excluded whereas smaller animals such as rodents (Rodentia) and hares (*Lepus* spp.) were able to enter all plots.

2.3. Data collection and preparation

We monitored individually marked conifer trees and the total number of trees in all plots twice per year; once during the onset of the growing period (i.e. spring, typically early April) and once at the end of the growing period (i.e. autumn, typically late September). We

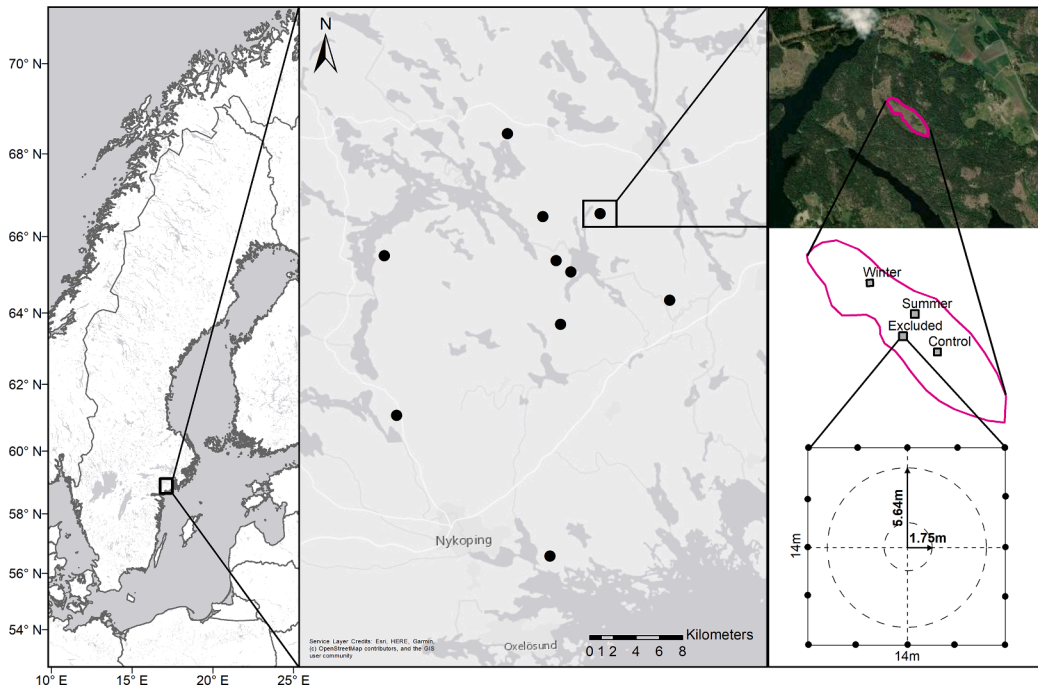


Fig. 1. Extent of study area with ten sites of former clear-cuts each containing four plots of randomized browsing treatments: *Excluded* (no browsing year-round), *Summer* (summer browsing only), *Winter* (winter browsing only), and *Control* (year-round browsing) treatment.

conducted the first complete measurements in spring 2016. To exclude potential effects on soil and growing conditions due to the use of heavy machinery when installing the wooden posts, we introduced a buffer zone of 2 m along the fence line inside each plot. Thus, we monitored trees within an area of $\sim 10 \times 10$ m in the center of each plot. From the collected data we extracted three variables to investigate further: the growth response of individually marked conifers, the demographic response over time (i.e., number of conifer stems in different height classes), and deciduous densities taller than individually marked conifers (Fig. 2).

2.3.1. Growth response of individually marked conifers

We measured height and recorded fresh deer damage (defined as apical leader browsing, bark damage on the stem, and stem breakage during the latest season) of individually marked pine and spruce trees inside each plot. We divided each plot into four quarters (Fig. 1) and marked up to four trees for each species in each quarter depending on the tree species with which the clear-cut was regenerated (i.e., four pine trees and one spruce tree per quadrant in stands regenerated with pine, and vice versa in stands regenerated with spruce). Individual trees were marked with small cable ties at the bottom of the stem as soon as trees were at least 10 cm tall. During each seasonal inventory, we marked new individuals that we found fulfilling this height criterion unless we

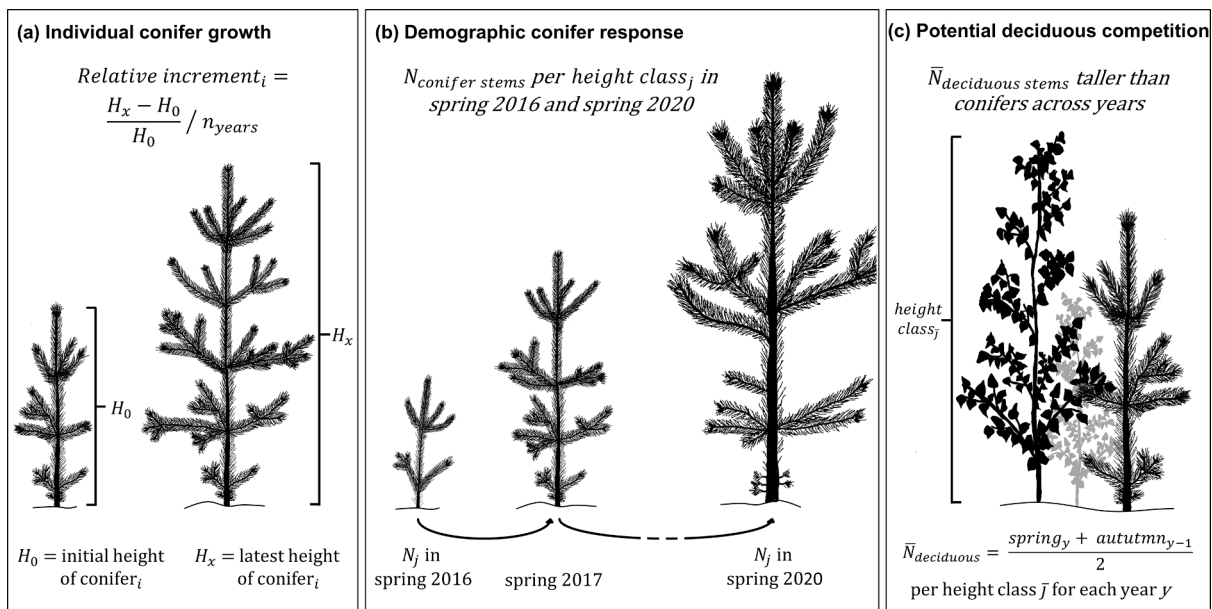


Fig. 2. Graphical overview of the three response variables representing (a) individual conifer growth (i.e. relative increment), (b) demographic conifer response (i.e. shift to taller height classes), and (c) potential competition effects from deciduous trees (i.e. number of deciduous stems taller than conifers).

already had marked the maximum number of individuals in that quadrant. Furthermore, individuals that died were replaced by new individuals, if available. Thus, the length of the period, during which we recorded height, varied among individually marked conifers (from 4 years for those marked at the start, to 0.5 years for those marked most recently). Therefore, we included only those individuals that we measured during at least four spring inventories (i.e., over a time period of ≥ 3 years: 2016–2020, 2016–2019 or 2017–2020) in the analyses of this study. Because we included planted and naturally recruited conifer individuals, and started following individual trees at slightly different times, the starting heights of individual conifers varied. To account for this, we calculated the individual's growth response to the browsing treatments as relative annual height increment (hereafter, relative increment). We defined relative increment as the difference between the latest spring height and the initial spring height divided by the initial spring height and the number of sampled years (Fig. 2a).

2.3.2. Demographic response

In addition to the measurements of individually marked conifers, we counted the total number of trees for pine, spruce, and the deciduous species downy birch (*Betula pubescens*), silver birch (*Betula pendula*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix spp.*), and oak (*Quercus robur*). We assigned each counted tree to a height class. We recorded seedlings of small height classes (1–5 cm, 6–20 cm, and 21–30 cm) within a circular area of 10 m² ($r = 1.78$ m, Fig. 1) around the center of each plot, whereas we recorded trees of taller height classes (31–50 cm, 51–100 cm, 101–150 cm, 151–200 cm, 201–250 cm, 251–300 cm, 301–350 cm, 351–400 cm) within a circular area of 100 m² ($r = 5.64$ m; Fig. 1) around the center of each plot. To test for differences in the demographic response of the two conifer species between the first spring measurements (i.e. spring 2016) and the latest spring measurements (i.e. spring 2020) between the browsing treatments (Fig. 2b), we aggregated the taller height classes into 31–50 cm, 51–100 cm, 101–200 cm, 201–300 cm, and 301–400 cm for pine and spruce.

2.3.3. Deciduous densities

We extracted the mean number of deciduous stems taller than the individually marked pine and spruce trees to be used in a separate analysis. Prior to this extraction, we multiplied the number of trees in the smaller size classes by the factor 10 to extrapolate to 100 m². We then calculated the number of deciduous stems per 100 m², per detailed height class, for each year y , and plot as the average between $spring_y$ and its previous $autumn_{y-1}$. We took the average between spring and autumn since deciduous numbers per height class varied between the seasonal measurements, likely a result of varying climatic conditions (e.g., winter conditions affecting seedling survival; Campbell et al., 2005) and browsing (e.g., treatments but also potential browsing by rodents and hares). We then assigned each height class its mean height value (e.g., the height class 31–50 cm is represented by 40 cm). For each year, we extracted the number of deciduous stems per 100 m² that were taller than the individual conifers. We did this separately for pine and spruce. In the last step, we calculated across the individual conifer's time series the average density of deciduous stems taller than individual pine and the average density of deciduous stems taller than individual spruce (hereafter, deciduous density; Fig. 2c).

2.4. Statistical analyses

2.4.1. Growth response of individually marked conifers

We used a linear mixed-effect model (*lme* function in R package *nlme*; Pinheiro et al., 2019) to test how 'browsing treatment' affected 'relative

increment', as a response, while including 'site' as random effect. We tested the relative increment of pine and spruce separately. Due to negative increment of a few pine trees (Fig. 3), we transformed the relative increment of pine to have a minimum value of 1 by adding the magnitude of the lowest relative increment of pine and 1 to all values. We then Tukey transformed the response of relative increment for both conifer species to assure normal distribution (*transformTukey* function in R package *rcompanion*; Mangiafico, 2020; $\lambda_{pine} = -1.1$, $\lambda_{spruce} = 0.175$). We calculated the variation explained by fixed and random effects using the *r.squaredGLMM* function (R package *MuMIn*; Barton, 2020).

2.4.2. Demographic response

To investigate the demographic response (i.e., number of conifer stems per height class) per treatment, we used a generalized linear mixed model with a poisson distribution accounting for zero-inflation (*glmmTMB* function in R package *glmmTMB*; Brooks et al., 2017)

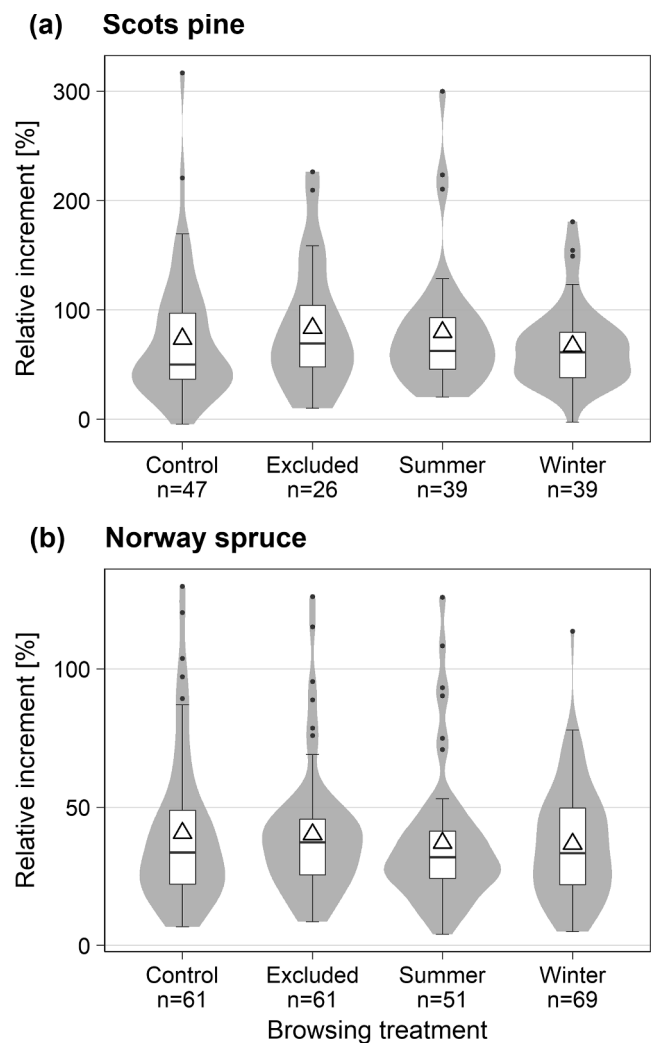


Fig. 3. Growth response of individually marked conifer trees presented as relative annual height increment (i.e. annual growth relative to initial height) per exclosure treatment across sites for (a) Scots pine and (b) Norway spruce presented as boxplots. Outlines of violin plots illustrate kernel probability density. Triangles illustrate mean values. Relative increment is based on individually marked trees that have been measured during ≥ 4 spring inventories, i.e. over a period of ≥ 3 years.

testing the fixed effects ‘browsing treatment’ and aggregated ‘height class’ and their interaction. We again included ‘site’ as random effect and tested pine and spruce separately from each other. We tested the demographic response for the latest spring measurement only (i.e. spring 2020) due to low sample sizes in the taller height classes in the first spring measurements (i.e. spring 2016). In spring 2016, most conifer stems across treatment plots were 30–50 cm tall (mean \pm SD number per plot for pine: 3.5 ± 6.2 , and for spruce: 5.7 ± 6.4) with only a few conifer stems being 50–100 cm tall (mean \pm SD number per plot for pine: 0.7 ± 3.0 , and for spruce: 0.9 ± 2.1 ; Fig. 4a + c). Due to low sample sizes in the tallest height classes in spring 2020, we excluded the height classes taller than 300 cm for pine (Fig. 4b) and taller than 200 cm for spruce (Fig. 4d) from these analyses.

2.4.3. Deciduous densities

In a last analysis, we used the same generalized linear mixed model setup as for the analysis of the demographic response. We fit the rounded response (i.e. integer) of ‘deciduous density’ taller than individual pine and spruce with the fixed factor ‘browsing treatment’. We included ‘site’ as random effect and tested how the browsing treatments affected

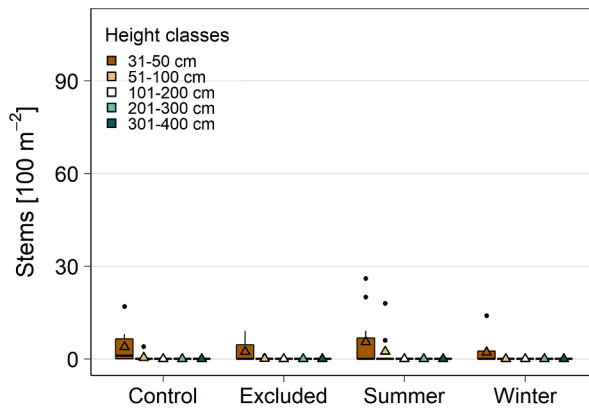
deciduous densities taller than pine or spruce separately for the two conifer species.

3. Results

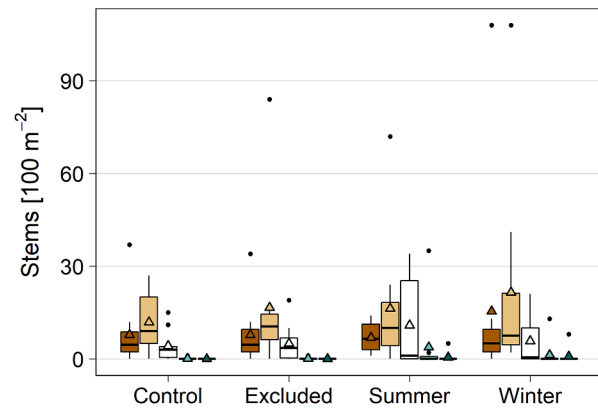
Over a time period of ≥ 3 years, we monitored in total 151 individual pine and 242 individual spruce trees. Out of these, we recorded fresh deer damage (i.e. apical leader browsing, bark damage on the stem, or stem breakage) on 23 of the pine and 14 of the spruce trees at least once during the study period across plots and sites. Of the individually marked pine trees, mean (\pm SD) annual damage levels per site were 9.44% (± 7.86) in the *Control* and 11.11% (± 11.79) in the *Winter browsing* plots. Of the individually marked spruce trees, mean (\pm SD) annual damage levels per site were 3.43% (± 5.89) in the *Control*, 1.48% (± 2.08) in the *Winter browsing*, and 3.88% (± 8.65) in the *Summer browsing* plots (see also Appendix, Table A.1). Deer damage occurred neither on pine in the *Summer browsing* plots nor on pine and spruce in the *No browsing* plots. In spring 2020, 4.5 years after the experimental start, silver birch was the most abundant tree species and pine was more abundant than spruce across treatments (Table 1). Furthermore, tree

Scots pine

(a) spring 2016

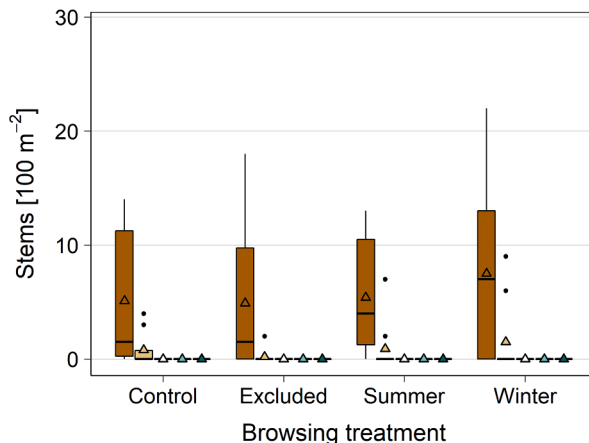


(b) spring 2020



Norway spruce

(c) spring 2016



(d) spring 2020

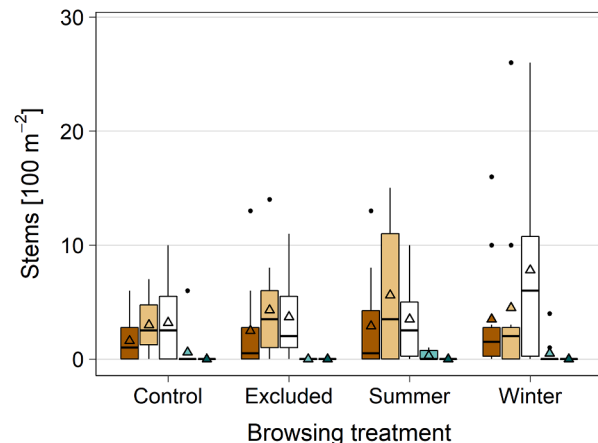


Fig. 4. Demographic responses of the two conifer species presented as the number of stems [100 m^{-2}] per aggregated height class per browsing treatment across sites for Scots pine in (a) spring 2016 and (b) spring 2020 and for Norway spruce in (c) spring 2016 and (d) spring 2020. Triangles illustrate mean values.

Table 1Mean (\pm SD) tree density per tree species represented by stems > 30 cm per 100 m^2 for each browsing treatment across sites in spring 2020.

Species	Browsing treatment			
	Control	No browsing	Summer browsing	Winter browsing
Scots pine	24.0 (± 22.6)	29.5 (± 39.3)	38.4 (± 42.4)	44.8 (± 72.5)
Norway spruce	8.4 (± 5.6)	10.5 (± 7.2)	12.3 (± 12.6)	16.3 (± 14.5)
Silver birch	63.3 (± 78.7)	67.3 (± 52.7)	85.8 (± 120.7)	83.8 (± 76.0)
Downy birch	9.1 (± 14.0)	68 (± 171.7)	16.4 (± 27.6)	38.9 (± 61.8)
Rowan	0.4 (± 1.3)	5.0 (± 4.3)	0.9 (± 2.5)	2.2 (± 3.7)
Aspen	13.9 (± 22.8)	14.9 (± 20.6)	15.2 (± 21.1)	41.4 (± 58.0)
Salix spp.	4.0 (± 5.5)	14.8 (± 12.4)	2.9 (± 4.3)	32.4 (± 46.2)
Oak	0.6 (± 1.3)	1.0 (± 1.1)	0.2 (± 0.4)	0.4 (± 0.7)

densities of both conifer species and a few deciduous tree species (e.g. silver birch) were highest in the *Summer* and *Winter* browsing plots, although with rather high standard deviations (see [Table 1](#)).

3.1. Growth response of individually marked conifers

The individual growth response (i.e. relative increment) of marked pine trees ($t < 1.3$, $p = 0.200$) and spruce trees ($t < 1.1$, $p = 0.272$) did not differ among browsing treatments. Thus, the variation explained by the fixed effect 'browsing treatment' was low (fixed effect: $R^2_{\text{pine}} = 0.59\%$; $R^2_{\text{spruce}} = 0.42\%$), whereas the variation explained by the random effect 'site' was higher but differed between pine and spruce (random effect: $R^2_{\text{pine}} = 50.24\%$; $R^2_{\text{spruce}} = 26.46\%$).

3.2. Demographic response

In spring 2020, the number of pine stems was highest in the 51–100 cm height class in both the *Control* and *No browsing* plots ($z \geq 2.0$, $p \leq 0.050$; Appendix, Table A.2; [Fig. 4b](#)). In the *Winter* browsing plots, most pine stems occurred in the height classes 31–50 cm and 51–100 cm ($z \geq 2.5$, $p \leq 0.011$), whereas in the *Summer* browsing plots, most pine stems occurred in the height classes 51–100 cm and 101–200 cm ($z \geq 4.4$, $p \leq 0.001$; Appendix, Table A.2; [Fig. 4b](#)).

The number of pine stems in the 31–50 cm and 51–100 cm height class was highest under *Winter* browsing compared to all other browsing treatments ($z \geq 2.5$, $p \leq 0.014$), whereas the number of pine stems in the 101–200 cm height class was highest under *Summer* browsing ($z \geq 3.4$, $p \leq 0.001$; Appendix, Table A.3; [Fig. 4b](#)). The number of pine stems in the 201–300 cm height class was higher under *Summer* and *Winter* browsing than under year-round (*Control*) and *No browsing* ($z \geq 3.5$, $p \leq 0.001$; Appendix, Table A.3; [Fig. 4b](#)).

The number of spruce stems did not differ between the height classes 31–50 cm, 51–100 cm, and 101–200 cm in the *Control* and *No browsing* plots in spring 2020 ($z \leq 1.2$, $p \geq 0.221$; Appendix, Table A.2). In the *Summer* browsing plots, most spruce stems occurred in the 51–100 cm height class ($z \geq 2.3$, $p \leq 0.022$), whereas in the *Winter* browsing plots, most spruce stems occurred in the 101–200 cm height class ($z \geq 2.4$, $p \leq 0.015$; Appendix, Table A.2; [Fig. 4d](#)). Thus, more spruce stems grew taller under the *Winter* as compared to the *Summer* browsing treatment, which is contrary to pine.

The number of spruce stems in the 31–50 cm height class did not differ between any of the four treatments ($z \leq 1.3$, $p \geq 0.208$; Appendix, Table A.3). However, the number of spruce stems in the 51–100 cm height class was higher in the *Summer* browsing than in the *Control* and *No browsing* plots ($z \geq 2.4$, $p \leq 0.017$), whereas the number of spruce stems in the 101–200 cm class was highest under *Winter* browsing ($z \geq 3.9$, $p \leq 0.001$; Appendix, Table A.3; [Fig. 4d](#)).

3.3. Deciduous densities

For pine, we detected the highest density of deciduous trees, which were taller than pine, in plots with only *Winter* browsing ($z \geq 10.5$, $p <$

0.001; [Fig. 5a](#)). Deciduous density did not differ significantly among the other browsing treatments ($z \leq 0.8$, $p \geq 0.400$).

For spruce, we detected the highest density of deciduous trees, which were taller than spruce, in the *No browsing* plots ($z \geq 6.1$, $p < 0.001$). Deciduous density was higher in the *Winter* than in the *Summer* browsing plots ($z = 8.8$, $p < 0.001$). We detected the lowest deciduous density in the *Control* plots ($z \geq -4.3$, $p < 0.001$).

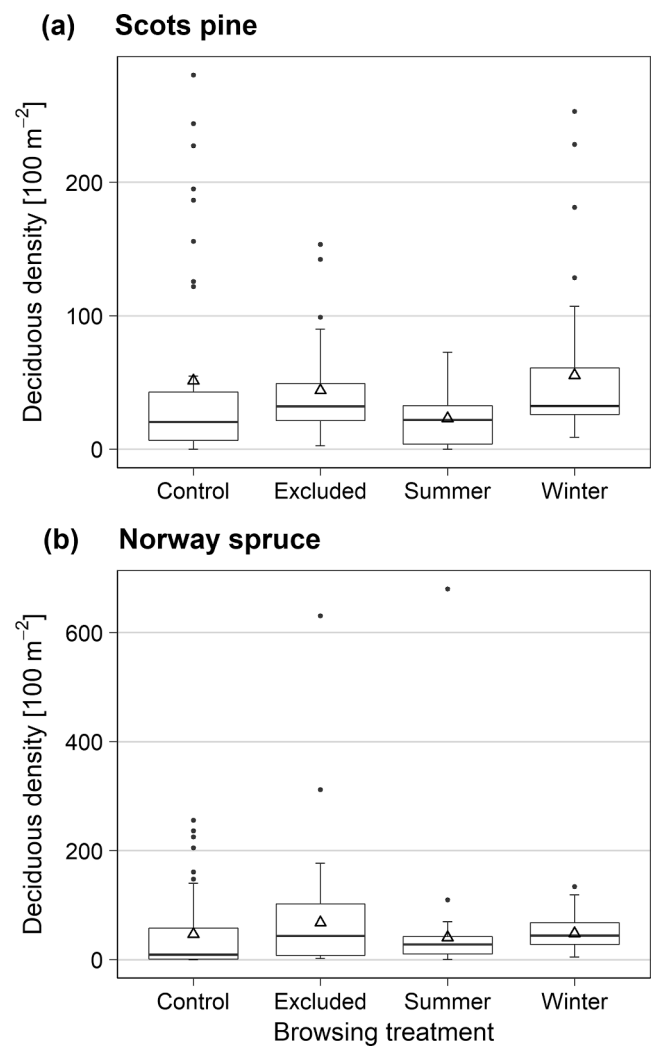


Fig. 5. Potential competition from deciduous density presented as deciduous stems taller than individually marked (a) Scots pine and (b) Norway spruce. Triangles illustrate mean values.

4. Discussion

We identified no differences in terms of individual growth response (i.e. relative increment) or demographic response (i.e. number of stems per height class) for pine or for spruce between the *Control* and *No browsing* plots. A similar result was previously reported by Speed et al. (2013), where neither growth of pine, nor of spruce, differed between a control and fully excluded browsing treatment. Furthermore, McLaren et al. (2009) reported that conifer growth was compromised by increased competition of deciduous trees when browsing was fully excluded. Thus, the complete absence of browsing does not necessarily improve conifer growth and this is most likely due to increased plant-plant-competition (Kuijper et al., 2010; McLaren et al., 2009; Stokely and Betts, 2020). Interestingly, overall densities of both conifer species seemed higher in the *Summer* and *Winter browsing* plots compared to the *Control* and *No browsing* plots, suggesting that seasonal fencing benefits conifer recruitment. These effects had, however, a high variation around the means. Therefore, this result should be interpreted with care. Over the next years, we will continue to monitor the experiment and see whether this effect of seasonal fencing on conifer recruitment becomes stronger.

4.1. Growth response of individually marked conifers

The relative increment of pine and spruce was not affected differently by *Summer* and *Winter browsing* for either conifer species, which was contrary to our expectations. Instead, a large variation of relative increment was explained by the random effect 'site'. Site specific factors might be more influential on the growth response of plant species, e.g. micro-climate (Mazza et al., 2014) or the surroundings of sites (Jalkanen, 2001). Furthermore, browsing pressure has been reported to be highly variable among sampling locations (Szwagrzyk et al., 2020). Alternatively, this study might have captured a too short time series after clear-cutting to detect clear effects in relative increment of individuals between the browsing treatments. The direct impact of ungulates on tree regeneration might increase only during later growth stages, whereas tree regeneration is dominantly affected by abiotic conditions during early growth stages (Kuijper et al., 2010). According to Jalkanen (2001), the impact of ungulate damage in boreal forests in southern Finland is highest for trees 100–200 cm in height and 10–20 years in age, however more heavily damaged are often smaller-sized trees (Charco et al., 2016). In this study, many conifer trees were still below 100 cm. Thus, the impacts of browsing on the individual growth response might not have occurred yet. Alternatively, we could not detect impacts of browsing since we analyzed the relative increment of individual conifers, whereas our demographic approach, which rests on the absolute differences in height, did show significant differences.

4.2. Demographic response influenced through potential deciduous competition

We detected a clear shift in conifer demography with differences among the browsing treatments. After only 4.5 years, *Summer* and *Winter browsing* led to different demographic responses of both conifers, even though forest regeneration is a long-term process (Speed et al., 2013). Interestingly, not only growth of the more palatable conifer species pine was affected but also of the less palatable spruce. Already Allen et al. (1984) state that less palatable species might also be affected by ungulate browsing.

For pine, we detected the highest density of deciduous trees, taller than pine, in the *Winter browsing* plots, and in these same plots, fewer pine trees grew to taller height classes than in the *Summer browsing* plots. We suggest that three, non-exclusive, mechanisms could be potentially driving this scenario. First, our results indicated that annual deer damage levels of pine were higher during winter than during summer, potentially resulting in shorter pine stems in the *Winter browsing* plots,

and at the same time leading to a higher deciduous density taller than pine as compared to the *Summer browsing* plots. Second, a high deciduous density in the *Winter browsing* plots might represent a high forage availability but a low forage quality during winter. According to selectivity rankings, birch *spp.*, the main deciduous species in this study, is often avoided during winter (Shipley et al., 1998; Jalkanen, 2001; Bergqvist et al., 2018) and diet analyses show that both moose and the smaller deer species select against broadleaved species (e.g., birch *spp.*) during winter (Spitzer, 2019). Thus, ungulate herbivores increase the browsing pressure on the higher quality forage pine in the presence of birch (Heikkilä and Härkönen, 1993). This mechanism can be called neighbor contrast susceptibility where browsing on the focal plant species increases due to avoided neighboring plant species (Champagne et al., 2016). Third, plant-plant-competition might be the driving mechanism (Kuijper et al., 2010; Stokely and Betts, 2020). Most broadleaf tree species respond with greater heights and basal diameters to excluded ungulate browsing (McLaren et al., 2009). However, pine is a light-demanding species where growth is reduced through shading (Bachofen et al., 2019). During winter, deciduous species are generally consumed below availability by all deer species, whereas they are consumed near or above availability during all other seasons including summer (Spitzer, 2019); for example, silver birch leaves are consumed as summer food by moose (Bergström and Danell, 1995). Thus, deciduous species are an important part of ungulate summer diets. Excluding summer browsing and allowing for *Winter browsing* only results in generally higher deciduous densities overtopping pine. Through competition from the deciduous species, pine growth might be reduced and additionally, pine might be kept longer within the susceptible browsing height (Danell et al., 1991). Herbivore browsing on deciduous trees during summer instead decreases the recruitment of competing trees and leads to increased pine growth (Vuorinen et al., 2020) as detected with a higher demographic growth response in the *Summer browsing* plots. In this case, trees might grow quicker above browsing height in the future (Stokely and Betts, 2020) decreasing the competitive advantage for less preferred species such as deciduous trees during winter (Tremblay et al., 2007; Spitzer, 2019). Thus, we conclude that pine stems in the *Winter browsing* plots are influenced by both ungulate browsing and competition (Stokely and Betts, 2020).

In the *Control* plots, the demographic growth response of pine did not differ from the *Winter browsing* plots. Thus, it can be concluded, that pine was mainly browsed during winter since our results also indicate higher levels of deer damage under *Winter browsing*, whereas damage levels were zero under *Summer browsing*. Of the different ungulate species in the study area, moose is the species whose diet contains most conifers while preferring pine over spruce (Milligan and Koricheva, 2013; Shipley et al., 1998). Thus, pine growth can be expected to be limited mainly through moose browsing during winter, whereas the overall ungulate consumption of deciduous species during summer (Spitzer, 2019) might regulate plant-plant competition.

For spruce, in contrast to pine, we found more trees in taller height classes in the *Winter browsing* plots compared to the *Summer browsing* plots. This suggests that spruce might be less influenced by the plant-plant-competition mechanism we outline above, which fits with spruce being a shade-tolerant species in contrast to pine (Heiskanen, 2004). Furthermore, deer damage occurred less frequently on individual spruce than pine, thus limiting growth to a lower extent. Spruce is rarely browsed (Speed et al., 2013; Szwagrzyk et al., 2020). The proportion of spruce in ungulate diets is usually low and the species is consumed below availability by all ungulate species in all seasons (Spitzer, 2019). According to Vuorinen et al. (2020), climatic factors and tree height are the main drivers for the growth of less preferred conifer tree species. Thus, spruce was potentially less affected by browsing. Instead, the micro-climate has an important impact on spruce (Langvall and Örlander, 2001) and shading from neighboring trees (e.g. when summer browsing is excluded) might protect spruce from frost and positively affect its growth (Heiskanen, 2004).

Often, effects of plant-plant-competition are regulated through pre-commercial thinning (PCT) to increase tree growth (Härkönen, 1998). Our results support the idea that ungulates might provide an ecosystem service by reducing plant-plant-competition through browsing (Stokely and Betts, 2020), thus reducing the need for PCT and the associated costs. However, the effects of direct browsing on conifers (e.g., *Control*) and indirect plant-plant-competition (e.g., *No browsing*) seemed to affect conifer growth similarly. Thus, the service associated with decreased competition through browsing was cancelled out by the disservice of browsing on conifers. Limiting only winter browsing on pine and allowing for summer browsing on deciduous trees, might reduce the competition from deciduous species (Härkönen, 1998), which resulted in a higher demographic response of pine in this study. This study, provides insights into the direct and indirect effects of browsing, which may inform discussions around fencing as a possible management tool. However, the relative importance of direct and indirect effects from browsing may well change over time. Elucidating the overall effects will require to follow stands throughout the period when susceptible to browsing, while taking effects of PCT into account. Plant-plant-competition might be reduced via PCT. However, PCT might also result in a reduced amount of alternative, preferred forage during summer (i.e. deciduous species), which could theoretically increase summer browsing on pine. These effects remain to be explored.

5. Conclusions

During the early stages of tree recruitment in even-aged forest management, a full exclusion of ungulate browsing did not enhance the growth of conifers in comparison to plots which could be accessed by ungulates year-round. Future research should investigate the detailed impacts of browsing and plant-plant-competition on tree growth. The two conifer species responded slightly differently to *Summer* versus *Winter browsing*. The different responses of pine and spruce might be dependent on their differences in palatability, their ability to tolerate plant-plant-competition (i.e., their shade tolerance), but potentially also associational effects.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119314>.

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