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ORIGINAL PAPER

Factors affecting admixed pedunculate oak growth under heavy browsing by deer: benefits from inter- and intraspecific neighbourhoods

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Abstract

One of the most important ecosystem processes, especially in temperate and boreal forests, is herbivore browsing. In this study, we tested five hypotheses: (H1) oak tree density would positively affect their height; (H2) despite severe browsing pressure, the height of oaks would increase with the age after planting; (H3) oaks growing among the planted pines would be taller than those among the sown ones; (H4) the growth of single oak saplings or of oak nests would be positively affected by the height of the pines growing in the immediate neighbourhood of the oaks; and (H5) the oak height would be affected by the location within a nest and oaks growing in the central zone would be taller than the others. The study was conducted in the Piska Forest in the north-eastern part of Poland. We established three variants of experiment. In the first variant, oaks were planted individually. In the second and third variants, oaks were planted in small nests. The second and third variants differed in the spacing of the nests: 8 × 8 m and 6 × 6 m, respectively. The division into the sub-variants referred to type of pine regeneration. In the first sub-variant, Scots pine was planted. In the second, pine was sown. In general, oaks growing within nests were significantly taller than those planted individually in the Scots pine rows. Despite heavy browsing, oak height consistently increased during the course of the study. Oak height also depended on the type of pine regeneration, and the mean height of oaks surrounded by planted pines was significantly higher than that of oaks surrounded by sown pines (which, in average, was shorter). That was because the planted pines were taller than the sown ones. We found that Spearman's correlation coefficients were positive and significant between pine and oak heights in variants 2 and 3. Growth of oaks did not depend on their location within a nest. The results of the regeneration method of oak (single vs nest and few vs many nests) are modified by browsing. The best method found in the heavy browsing circumstances was planting oaks in many nests within successful pine regeneration (providing the oaks with protection against the browsing). The pine will provide the most efficient protection if regenerated a few years before the oaks.

Keywords *Quercus robur* · *Pinus sylvestris* · Forest regeneration · Deer · Browsing

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Introduction

Ungulate browsing is one of the most important processes in ecosystems, especially in temperate and boreal forests (Zamora et al. 2003; Motta 2003; Saha et al. 2012; Faison et al. 2016). Browsing has been reported as a severe problem in artificial and natural regeneration of forests in many countries (Motta 1996; Drexhage and Colin 2003; Hegland et al. 2013). The impact of browsing depends, among other factors, on tree species and ecosystem composition (Kullberg and Welander 2003). The growth of trees such as birch, beech and especially oak and fir is negatively affected by roe deer and red deer browsing (Van Hees et al. 1996; Cote et al. 2004; Kupferschmid 2018). The effects of browsing are greatly influenced by the quality of the habitat, the time when the damage occurs (Canham et al. 1994), the age of the seedling (Harmer 2001; Jones et al. 2009), the landscape mosaic (Ward et al. 2008), and the intensity of browsing (Kupferschmid 2018) as well as the population density of ungulates (Bergquist and Orlander 1998; Gill 2000). Constantly increasing deer populations in many countries suggest that in the future, the problem of ungulate pressure on forest ecosystems will increase (Cutini et al. 2011). One browsing incident usually does not have much impact on the height or biomass of the deciduous and coniferous tree species (Hoogesteger and Karlsson 1992). Slightly browsed trees can even grow taller than their undamaged counterparts (Kullberg and Welander 2003). Repeated browsing is more dangerous for trees, and very intensive browsing can even cause their death (Harmer 2001; Annighöfer et al. 2015).

One of the main species damaged by herbivores is oaks (Jensen et al. 2012). Browsing reduces the annual elongation of oak shoots, number of flushes (Chaar et al. 1997), and root and shoot weight (Kullberg and Welander 2003) and has negative impact on the availability of nutrients and hormones (Frost and Hunter 2004). Browsing of oaks leads to the destruction of the main stem (Bergquist et al. 2003), stimulates the development of several main stems (Harmer 2001), forms persistent forks and deformed stems, and decreases diameter growth (Chaar et al. 1997). These defects are often considered to be more serious than the growth loss (Eiberle 1975).

Trees that have been browsed are more exposed to further browsing by ungulates (Pepin et al. 2006). Oak can survive repeated browsing of the main shoot by sprouting or remaining in a suppressed state for several years (Drexhage and Colin 2003; Götmark and Kiffer 2014). Browsed oaks allocate a main part of their resources in the roots. Well-developed root systems are important as a source of carbohydrates for oak regrowth (Gill 2000). The height growth is influenced by tree vigour and apical control of the oak height (Drexhage and Colin 2003). In addition, browsing stimulates diameter growth at the root collar which is a zone of high meristem activity (Drexhage and Colin 2003). Winter browsing had little effect on growth and survival of pedunculate oak seedlings (Canham et al. 1994; Kullberg and Bergström 2001). Sessile oak (*Quercus petraea* (Matt.) Liebl.) browsing increased the number of branches and leaf biomass (Drexhage and Colin 2003). However, opposite results were reported by Bideau et al. (2016), who found that deer browsing decreased the number of shoots. Thus, there is a lack of knowledge of the prolonged impact of ungulate browsing on trees.

In numerous studies, mostly simulated experiments, the short-term effects of browsing on seedling growth were examined (Harmer 2001; Halpern and Underwood 2006). Although fencing is an effective method of protection against browsing, it is too expensive to be widely used (Bradfer-Lawrence and Rao 2012). Therefore, more knowledge on regenerative growth under severe deer pressure is urgently needed.

Most of foresters' effort is put towards increasing the proportion of deciduous tree species in managed coniferous forests (Annighöfer et al. 2015). In Poland, oak species (pedunculate and sessile) cover 6.4% of the total forest area (according to volume) (Report of Forest State 2016). Together with European beech (*Fagus sylvatica* L.), native oak species increase the resilience of forests to disturbances (Farjon 2005). In addition, association with oak is beneficial for pine. For instance, the second layer of oak fosters the self-pruning of pine stems, positively influences the site conditions, and increases the volume of a stand (Spathelf and Ammer 2015). Oak is a natural element in Scots pine forests in temperate climate zones (Bernadzki et al. 1998). The pedunculate oak and Scots pine have similar ecology. Both of them are light demanding and require open forest structures for sapling growth (Ellenberg 1996).

This paper presents the results from a 10-year study on the growth of heavily browsed oak penduculate. Thereby, we focused on the effect of repeated browsing on the growth of young oak trees growing in pine stands. Our general assumption was that spatial–temporal distribution of browsing incidence will affect oak height. Deer browsing tends to be inversely related to tree density (Lyly and Saksa 1992; Reimoser et al. 2009; Gerhardt et al. 2013). If so, the oak density should also affect their height. In our previous study (Borkowski et al. 2017), we have reported that the oak browsing incidence was among others affected by the height of pine patches surrounded the oaks. Szymański (1977) suggested that in the case of oaks growing within nests under browsing pressure, the central trees are more resilient thanks to the protective influence of the surrounding trees, however, that was not verified. The aim of the study was to answer the question of how oak height will be affected by the following factors: (i) the oak tree density, (ii) plantation age, (iii) pine height at the patch scale, (iv) pine height at the scale of single oak sapling/nest, and (v) location of the oak trees within a nest.

In the present study, we tested following five hypotheses: (H1) the oak tree density would positively affect their height; (H2) despite severe browsing pressure, the height of oaks would increase with age after planting; (H3) oaks growing among the planted pines would be taller than those among the sown ones; (H4) the growth of single oak saplings/nests would be positively affected by the height of the pines growing in the immediate neighbourhood of the oaks; and (H5) oak height would be affected by the location within a nest and that the oaks growing in the central zone would be taller than the others.

Materials and methods

Study area

The study was conducted in the Piska Forest (area 100,000 ha) in the north-eastern part of Poland. Scots pine is the main tree species in the area, with the admixture of auxiliary species such as silver birch (*Betula pendula* Roth.), Norway spruce (*Picea abies* (L.) Karst), and black alder (*Alnus glutinosa* Gaertn.) on moister sites. In the Pisz Forest District, which is a part of the Piska Forest, a hurricane damaged 10 thousand hectares of forests in 2002. Almost the whole area of the windthrow was cleared and replanted by Scots pine (*Pinus sylvestris* L.) and pedunculate oak. Scots pine was planted in rows, and additional tree species were planted individually. The main area of artificial planting was fenced because of the high pressure of herbivores. Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) densities during the study period were moderate: 3–4, 3–3.5 ind. per 100 ha, respectively, while that of moose (*Alces alces*) was rather low (0.2–0.5 ind. per 100 ha) (Pisz Forest District Headquarters). Deer densities were estimated by the Pisz Forest District using drive count method (Borkowski et al. 2011). Deer browsing on the plantations studied was heavy, and for several years of the study, all the oaks planted were browsed (see Fig. 3 in Borkowski et al. 2017). However, an area of 470 ha (Szast Protected Forest) was left to observe natural processes (Dobrowolska 2014). In the vicinity of the Szast Protected Forest, some area was designated for the experimental plots and was not fenced.

The mean annual temperature is 7 °C, and the mean annual precipitation is 541 mm (Lorenc 2005). Most of the precipitation falls in the summer. The growing season lasts only 190–200 days. Poor sandy soils dominate the Piska Forest.

Experimental design

The plots were established in 2006 on a clear-cut area after the windthrow in the Pisz Forest District. We established three variants. In each variant, oak was planted within the rows of Scots pine (Fig. 1). The initial spacing was 1.5 m between rows and 1 m between planted pines. In the first variant (V1) of the experiment (total area 8.88 ha), oaks were planted individually (as every tenth tree in a row). The spacing between oaks was approximately 10 m, and there were 900 oaks per ha. In the second (V2; 6.15 ha) and third (V3; 7.58 ha) variants, 21 oak seedlings were planted within nests (clusters) of 1 m^2 in size with a spacing of 0.25×0.25 m. The nest planting design was described by the Polish silviculturist Stanisław Szymański in the 1950s and 1960s (Szymański 1966, 1977). In V2, 2835 oak seedlings per ha were planted in 156 nests (Fig. 2). The spacing between nests was 8×8 m. In V3, 4830 oak seedlings per ha were planted in 277 nests. The spacing of the nests was 6×6 m (Fig. 2).

Each variant was split into two roughly equal parts (sub-variants). On the one part (sub-variants 1.1, 2.1, and 3.1), Scots pine was planted; on the other (sub-variants 1.2, 2.2, and 3.2), Scots pine was sown (Fig. 1). Pine sowing was generally unsuccessful in 2006, so it was repeated in spring 2007. Where necessary, additional pines were planted (in the part where pine was planted). In general, the areas of the planted pine were taller than those regenerated by sowing. One-year-old bare-rooted oak seedlings and 1-year-old pine seedlings were planted in all the variants. Seedlings of both species came from local provenances (from Pisz Forest District).

Data collection

The data on oak regeneration were collected in early spring from 2008 to 2015, except 2010 and 2012. The method for collecting the data on oak height depended on the variant of the experiment. In variant 1, each year, alongside 20 randomly chosen transects (10 among sown and 10 among the planted pines), 10 nearest oaks were measured. In variants 2 and 3, 50 nests of oaks were randomly selected (25 in planted and 25 in sown pines). The random variability of the nests was included into statistical analysis as a microhabitat effect (see "Statistical analysis" section). In each nest, the heights of all living oak trees were measured as the vertical height from the ground to the top of the tree. We determined the location of each oak within the nest (Fig. 2). Thereby, all oaks were classified into three zones: central (closest to the nest's centre), inner, and peripheral (close to the nest's edge). Thus, every zone was, in fact, a circular sector, and the width of each was approximately equal to one-third of a nest (circle) radius.

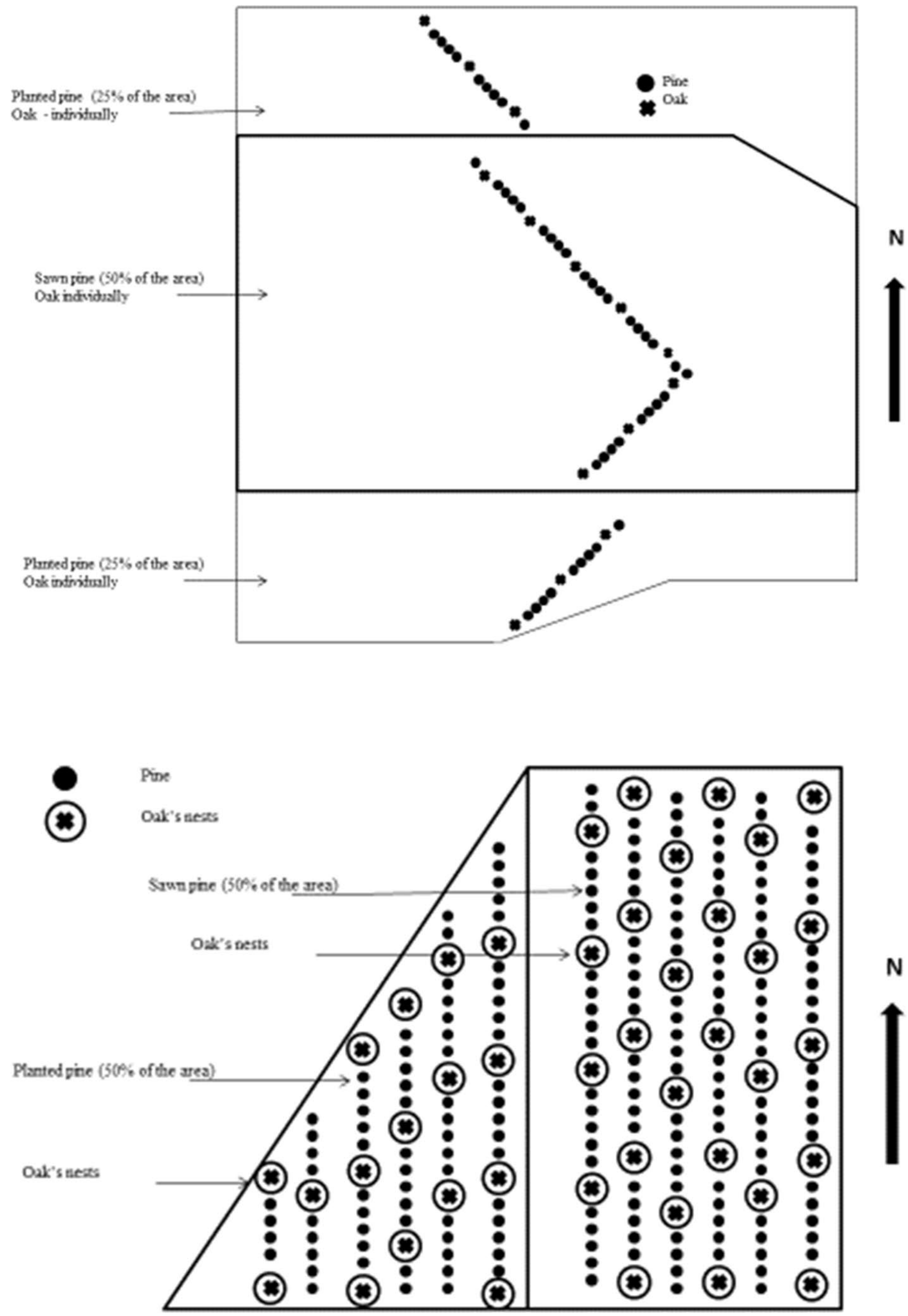

Fig. 1 The scheme of experimental plots, variant 1—oak planted individually between Scots pine rows; variants 2 and 3—oak planted in the nests. V1—spacing between the oaks approximately 10 m; V2—156 nests per ha (spacing between them 8 × 8 m); V3—277 nests per ha (6 × 6 m)

To additionally estimate the effect of the neighbouring pines sapling on oak height, we counted the number and measured the height of all pine trees growing within a radius of 5 m from a sapling or from a central point of the nest. Each time we randomly selected 75 saplings or nests in each variant. Data on the influence of neighbouring trees were collected for variant 1 in 2013 and 2015 and for variants 2 and 3 in 2012 and 2014. The data on browsing were collected in 2008–2015. The details of the data collection on browsing incidence were given in Borkowski et al. (2017).

Statistical analysis

We used a general linear model (GLMM) with log-normal distribution (Table 1, model 1) and post hoc Tukey–Kramer method ($P < 0.05$) to analyse the effects on oak height. We fitted as fixed effects the time after plantation, the three variants and the two sub-variants (planted, sown pine) and as random effect the presence of browsing nested within time after plantation.

To evaluate the effect of microhabitat (random variability of the nests) on the growth of oaks, we analysed the data

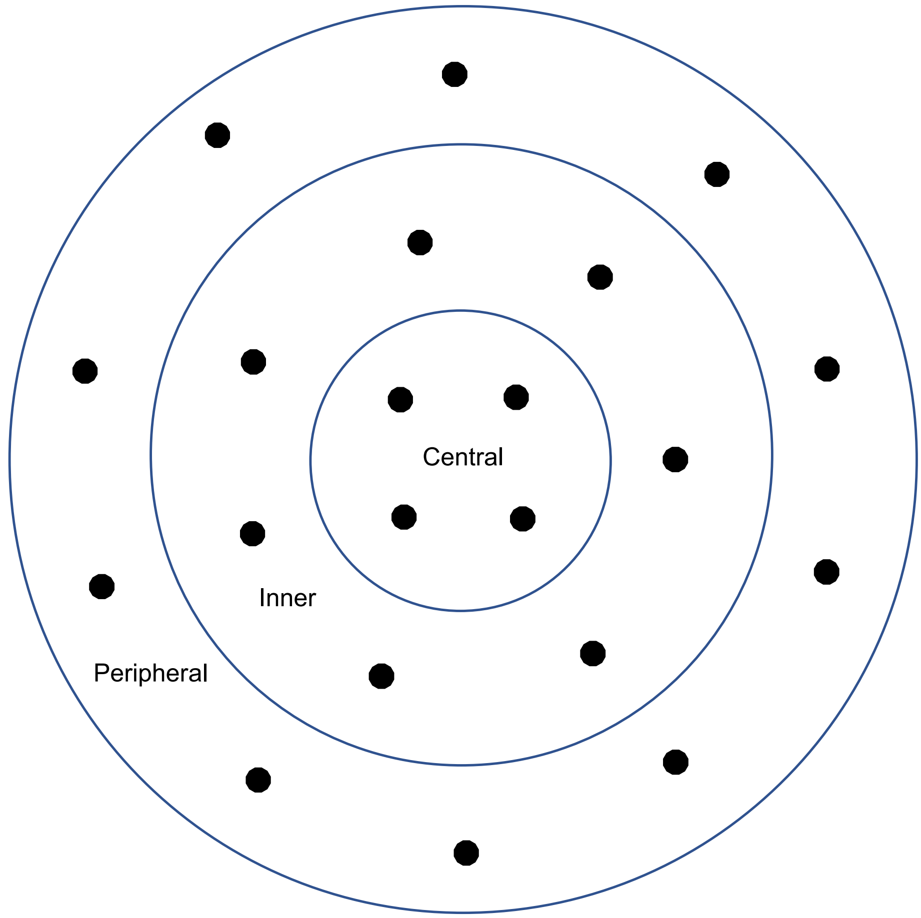

Fig. 2 The scheme of the oak nest layout (21 oak seedlings were planted in nests of 1 m^2 in size with a spacing of 0.25 × 0.25 m)

Table 1 The summary of all effects GLMM model including all variants (model 1) and including only variants 2 and 3 with nest location (model 2)

Effect	Model 1		Model 2	
	F	*p*	*F*	*p*
Variant—*A*	79.6	< 0.0001	139.7	< 0.0001
Sub-variant—*B*	23.4	< 0.0001	60.5	< 0.0001
A × *B*	8.6	0.0002	0.8	0.3697
Time after planting—*C*	175.5	< 0.0001	191.6	< 0.0001
A × *C*	5.6	< 0.0001	5.9	< 0.0001
B × *C*	3.0	0.0112	3.1	0.0093
Browsing (age)—*D*(*C*)	27.5	< 0.0001	37.9	< 0.0001
A × *D*(*C*)	2.1	0.0787	1.0	0.4056
B × *D*(*C*)	1.3	0.2180	2.9	0.0230
Nest location in an area	n/a	n/a	1.2	0.2803

from variants 2 and 3. In a second GLMM (Table 1, model 2), we thus included nest random variability within the variants as a further random effect. The rest of the factors were identical to model 1 (Table 1, model 2). A third GLMM (Table 3) included the factors from the second model as well as the location of oaks within a nest (three zones). Here, we used data only from 2015, the last year of our experiment. The percentage of occurrence of oak in height classes was compared using χ^2 tests for each height class separately. For analysing the amounts of tallest oak trees in 2015 (height class > 150 cm), we also used χ^2 tests. For analysing the influence of neighbouring pines on the oak height, Spearman's rank correlation was used. These calculations were done separately for the variants, i.e. for variants 2 and 3 with data of 2014 and for the variant 1 with data of 2015. All the calculations were done using STATISTICA software (TIBCO Software Inc., 2017).

Results

Factors affecting oak height at the plantation scale

All the fixed factors (variant of experiment, sub-variant—planted/sown pine), time after planting and their interactions and random effect of browsing nested within plantation significantly affected oak height (Table 1, model 1). However, the interactions browsing × variant and browsing × sub-variant were not significant ($p > 0.05$). Lack of significant interaction means that the influence of browsing on the oak height was the same regardless of the variant and sub-variant. In addition, the model showed that the effect of the microhabitat was not significant (Table 1, model 2).

Influence of oak density and type of pine regeneration method on the oak height

The average height of oaks was affected by the variant ($p < 0.0001$, Table 1). In general, oaks growing in variant 3 were significantly taller than oaks in variants 1 and 2 (Fig. 3). However, the differences between variants 1 and 2 were not significant ($p > 0.05$).

The oak height depended also on the type of pine reforestation (significant interaction in Table 1). The mean height of oaks surrounded by planted pines was significantly greater than that of oaks surrounded by sown pines. The differences in oak height depending on the pine reforestation method were modified by the variant of experiment (Table 1). In variants 2 and 3, oaks growing in planted pine were significantly taller than those in sown pine (Fig. 3). In variant 1, the height of oaks was similar between the two sub-variants. In summary, the highest oaks were growing in variant 3, sub-variant planted pines.

Oak height distributions in 2015 differed significantly between the variants, especially between variant 1 and the other two (Fig. 4). The percentage of the shortest trees (h < 50 cm) was significantly higher in variant 1 than in variants 2 ($\chi^2 = 26.8$; $p < 0.001$) and 3 ($\chi^2 = 32.4$ and $p < 0.001$). Similarly, the percentage of trees with heights of 50–100 cm was significantly higher in variant 1 than in variants 2 and 3. The number of trees with heights of 100–150 cm was significantly lower in variant 1 than in variants 2 ($\chi^2 = 26.8$; $p < 0.001$) and 3 ($\chi^2 = 42.5$ and $p < 0.001$). A similar trend was found for trees with heights > 150 cm, which were present at significantly lower proportions in variant 1 than in the other variants.

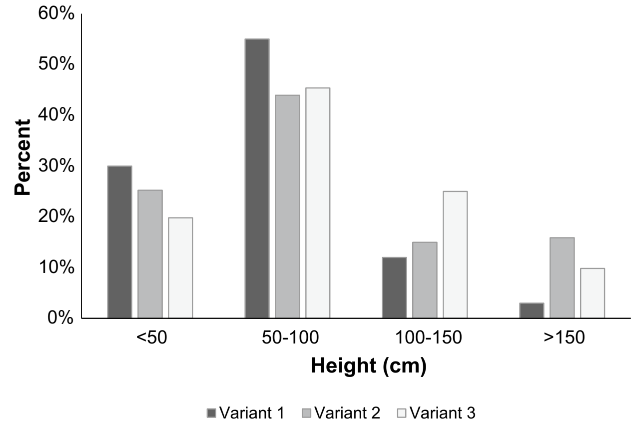

Fig. 4 Distribution of oak heights according to variants (variant 1—solitary, variant 2—nested, less dense, variant 3—nested, dense) in 2015

Influence of the time after planting on the oak height

Another factor influencing oak height was time after planting (Table 1, Fig. 5). There were no differences in oak height between the third and fourth years of oak growth. The same was observed between the sixth and eighth years of oak growth. In the other years, the mean oak growth

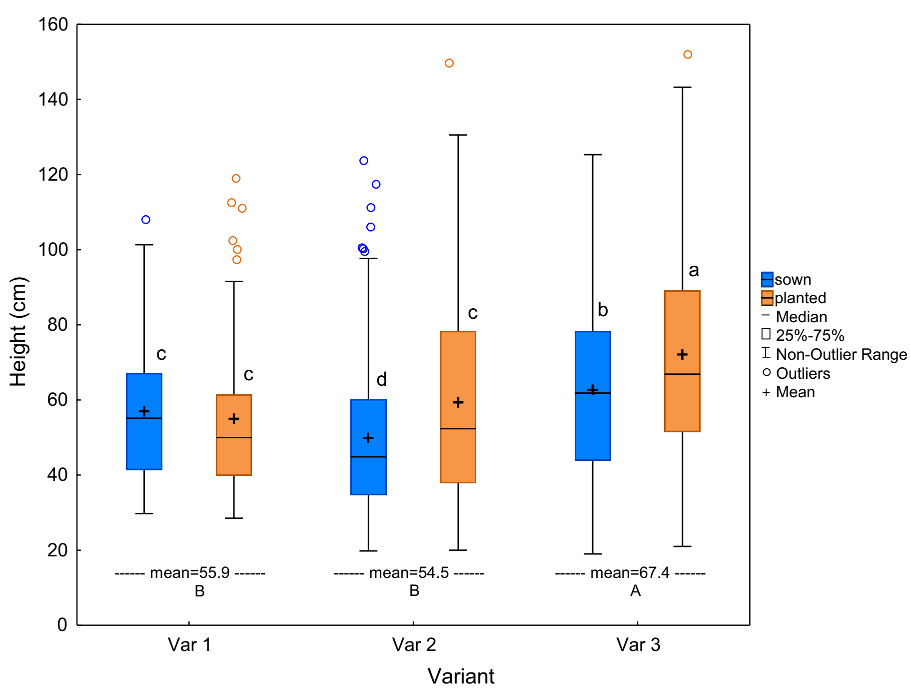

Fig. 3 Oak height depending on variant (variant 1—solitary, variant 2—nested, less-dense, variant 3—nested, dense) and sub-variant (Scots pine planting vs. sowing). The same letter shows no statistically significant differences at $p < 0.05$ according to Tukey–Kramer method (uppercase latter—main effect; lowercase latter—interaction effect)

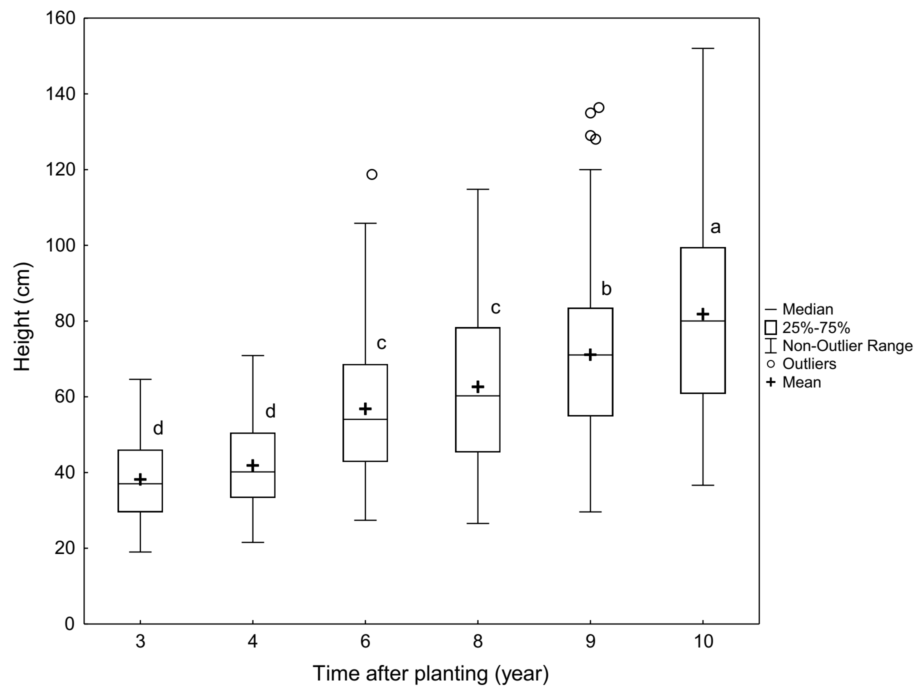

Fig. 5 Oak height depending on time after planting (all variants). The same letter shows no statistically significant differences at $p < 0.05$ according to Tukey–Kramer method

differed significantly from the previous years. In the tenth year after planting, mean oak height was twice that in the third year after planting. Oak height was also affected by the variant × time after planting interaction (Table 1). In general, the oaks growing in variant 3 were taller than those in the other variants (Fig. 6). The only exceptions were observed in the ninth year after planting, when the differences were not significant. In the third and fourth years after planting, oaks in variant 1 were significantly taller than those in variant 2; however, later that difference disappeared (Fig. 6). Another significant interaction was between the pine reforestation method and the time after planting (Table 1). At the beginning (third–fourth years after establishing the plantations), oak growth was similar in the two types of pine reforestation (Fig. 7). Beginning with the sixth year after establishing the plantations, oaks surrounded by the planted pines were significantly taller than those growing among the sown pines.

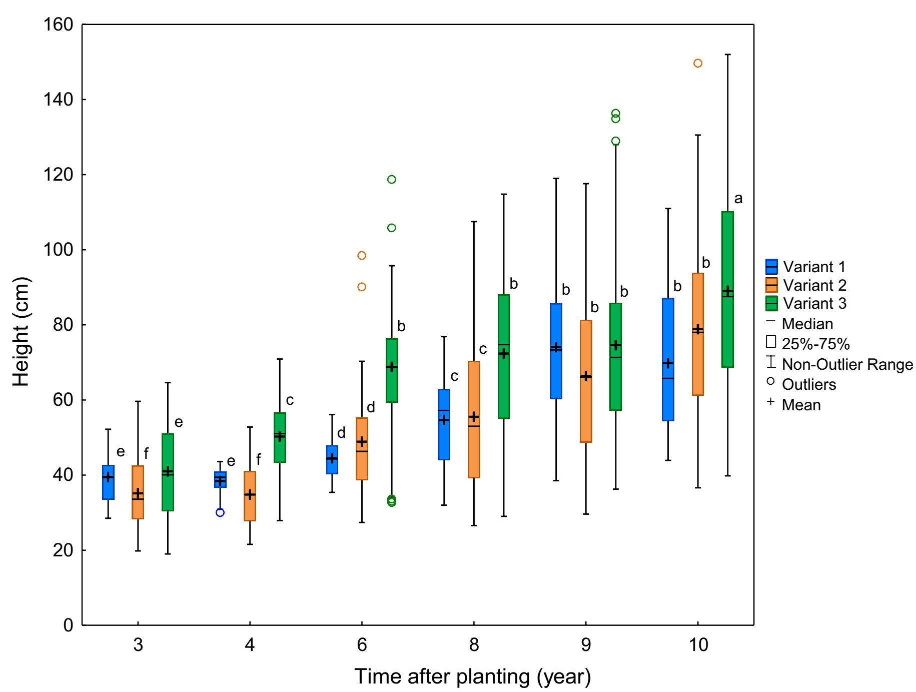

Fig. 6 Oak height depending on time after planting and variant (variant 1—solitary, variant 2—nested, less-dense, variant 3—nested, dense). The same letter shows no statistically significant differences at $p < 0.05$ according to Tukey–Kramer method

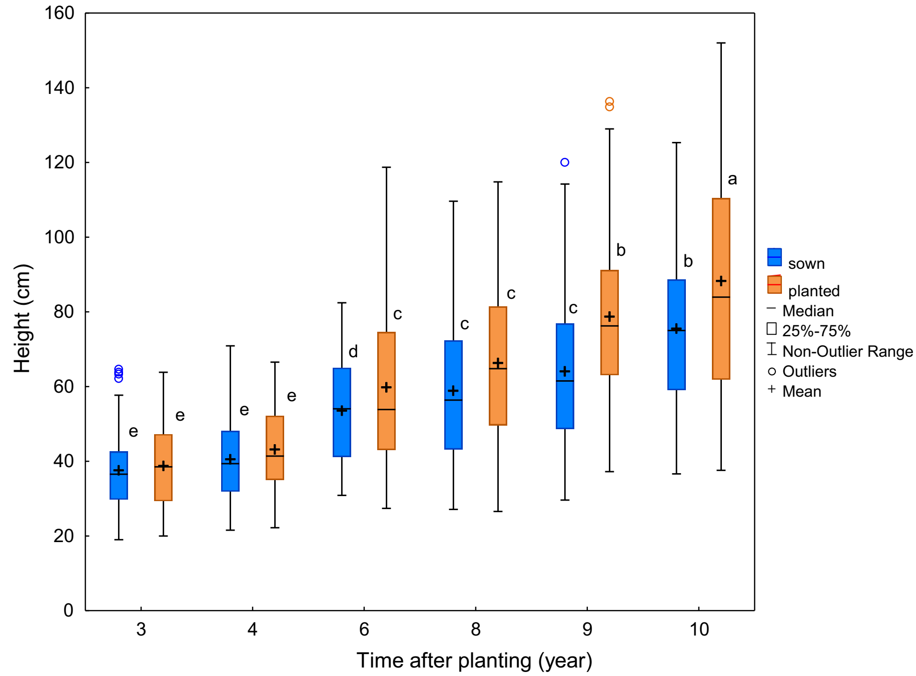

Fig. 7 Oak height depending on time after planting and pine regeneration (planting vs. sowing). The same letter shows no statistically significant differences at $p < 0.05$ according to Tukey–Kramer method

Despite the heavy browsing, in some years reaching 100% of the oak trees, average oak height consistently increased during the course of the study (Fig. 5). The model showed that browsing had a significant impact on oak height (Table 1). Three and 8 years after planting the browsed oaks were significantly taller than unbrowsed oaks (Fig. 8). This means that taller trees were selected by deer compared to shorter ones.

Influence of neighbouring pines

We found that Spearman's correlation coefficients between the average oak height (years 2014–2015) in an individual

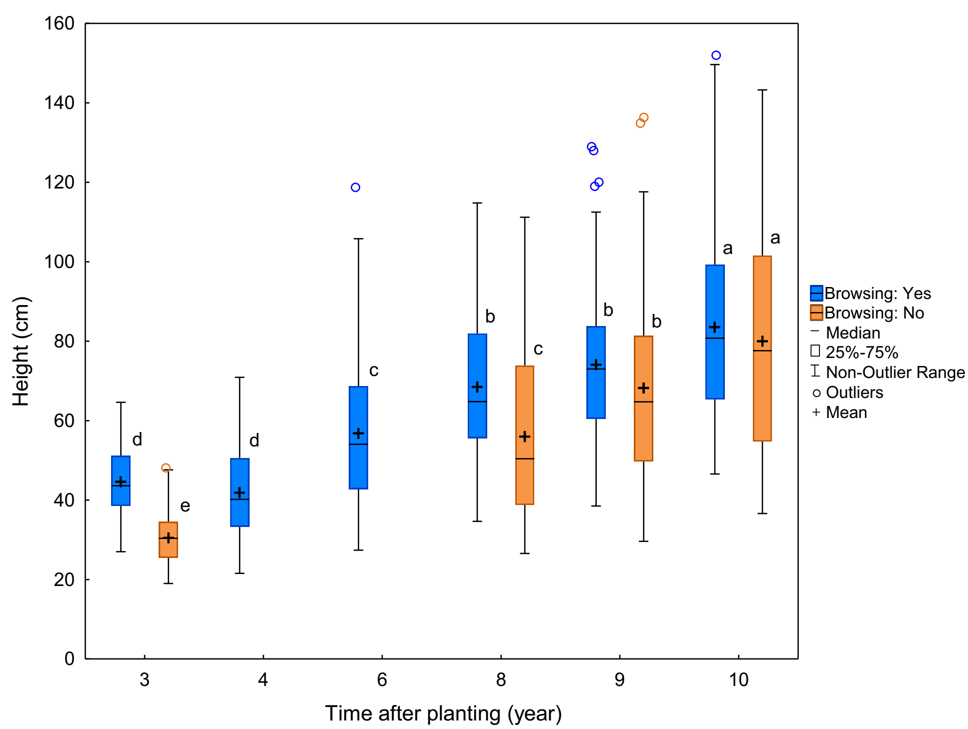

Fig. 8 Oak height depending on browsing nested within time after planting (all variants). The same letter shows no statistically significant differences at $p < 0.05$ according to Tukey–Kramer method

Table 2 Spearman's rank correlations (R) between density or the height of Scots pine and oak height in 2014 (variants 2 and 3) or 2015 (variant 1)

Variant of plantation	Trait	N	R	$t(N-2)$	p
Variant 1	Pine height	75	0.18	1.58	0.1182
	Pine tree number	75	−0.22	−1.89	0.0622
Variant 2	Pine height	74	**0.41**	3.79	0.0003
	Pine tree number	74	−0.17	−1.43	0.1584
Variant 3	Pine height	75	**0.44**	4.16	0.0001
	Pine tree number	75	−0.12	−1.04	0.3037

Significant correlation coefficient with $p<0.05$ is shown in bold

Table 3 The summary of GLMM including only variants 2 and 3 and location within the nest (data 42 only for 2015)

Effect	F	p
Variant (A)	3.39	0.0663
Sub-variant (B)	23.80	<0.0001
Location in the nest (C)	2.08	0.1265
Browsing (D)	1.93	0.1650
$A \times B$	8.55	0.0036
$A \times C$	0.99	0.3721
$B \times C$	0.24	0.7900
$A \times D$	0.95	0.3310
$B \times D$	12.65	0.0004
$C \times D$	1.75	0.1746
Nest location in an area	4.62	<0.0001

nest and the height of neighbouring pines were significant in variants 2 and 3 ($p<0.001$ in both cases; Table 2). With increasing pine height, the oak height also increased in both variants (2 and 3). For variant 1, the correlation was not significant ($p>0.05$; Table 2). Regarding the correlation between oak height and number of neighbouring pine trees, the Spearman coefficient was not significant in all variants.

Oak height depending on the location in a nest

In this analysis only, oaks from the last year of our experiment (2015) were considered. The growth of oaks did not depend on their location within a nest (Table 3). However, oaks were taller when surrounded by planted pines. The significant interaction between browsing × sub-variant confirmed our previous results that oaks that were browsed more often when surrounded by planted rather than sown pines because they were significantly taller (Table 3). We repeated the analysis for the trees taller than 50 cm. Nevertheless, location of the oaks within a nest had no significant influence on their height (in all cases, $p>0.05$).

Distribution of the tallest oak trees in the variants

As already mentioned, percentage of the tallest trees (> 150 cm in height) was significantly lower in variant 1 (3%) than in variants 2 and 3 (16 and 10%, respectively). Trees taller than 150 cm in year 2015 were absent from 46% and 52% of nests in variants 2 and 3, respectively (Table 4). Test χ^2 showed that the difference between variants was not statistically significant. In both variants, approximately one-third of the nests contained at least three oaks > 150 cm. The effective number of oak trees taller than 150 cm was 27, 454 and 483 for variants 1–3.

Discussion

Our study described the growth of oaks under heavy browsing pressure by ungulates (mainly deer). In 2009 and 2011, all the oak trees in the experimental plantations were browsed; afterwards, the browsing incidence began to decrease. Our analysis therefore did not focus on the comparison, but demonstrated the factors modifying the consequences of browsing for the oak height. Our data show that the height of an attractive species for deer can be highly diversified despite heavy browsing.

Factors affecting oak height at the plantation scale

Oak height was affected by the density of the species. Oaks growing at the highest nest density per ha (variant 3) were the tallest. They were significantly taller than oaks growing individually (variant 1) or within nests of lower density per ha (variant 2). The average oak height was not the best measure of their growth because in the nest variants, some trees were suppressed due to intraspecific competition, which decreased the mean height. When we instead used the distribution of oak trees in the height classes, the percentage of short trees was significantly larger in variant 1 than in variants 2 and 3. Conversely, oaks in the tallest

Table 4 Number of nests with 0 to ≥ 3 oak saplings out of 21 planting saplings that were taller than 150 cm 10 years after plantation (i.e. data from 2015)

Number of tall oaks	0		1		2		≥3	
	N	%	N	%	N	%	N	%
Variant 2	23	46	4	8	6	12	17	34
Variant 3	26	52	6	12	3	6	15	30

height class were several times more frequent in variants 2 and 3 than in variant 1. This enables us to conclude that despite similar browsing incidence in all the variants, tree density affected the growth of browsed oak trees and that in general, the consequences of deer browsing for the oak height were more visible in variants with low oak density. The difference in this respect was especially clear between variant 1 and the variants with nested oaks (2 and 3). Several case studies of nest plantings reported increased levels of browsing damage in nests versus row plantings (Gussone and Richter 1994; Weinreich and Grulke 2001). Although in our study, the growth of oaks was much better within nests than in rows, it is difficult to compare these results with previous studies because in our case, the differences in the method of planting were accompanied by differences in density. Young oak seedlings were generally highly susceptible to deer browsing (Götmark et al. 2005). Nahlik and Walter-Illes (1998) observed that beginning in the third year of growth, sessile oak is sensitive to pruning of the leading shoots, which results in retarded growth and height of the affected trees. Despite several years of intense browsing, the average height of oaks in our study increased each year. In addition, we found significant differences of browsed versus unbrowsed oaks over years. The taller oaks were browsed more frequently (Fig. 8), which indicates that taller trees were selected by the deer. Herbivores prefer taller trees because of their easier accessibility. In addition, they may be more vital, providing more energy (Price 1991a, b; Hartley et al. 1997). In our previous study (Borkowski et al. 2017), we documented that together with the growth of pine prethickets (starting from the eighth year after planting) oak browsing gradually began to decrease. Deer manoeuvrability and finding the oaks growing in the denser prethicket was probably more difficult. As a consequence, the browsing pressure dropped, and the height of oaks increased markedly.

Factors affecting oak height at the sub-variant scale

Oaks surrounded by sown pines were significantly shorter than oaks surrounded by planted pines. Sown pines in our study grew slower than the planted ones. Ackzell (1993) reported that the sum of height of all pines (variable explaining the fulfilment of regeneration) was almost three times higher for planting than for sowing. The second reason for slower growth of sown pines in our study was a problem with the germination (see *Experimental design*). Since the sown pines were shorter, the oaks growing among them were more frequently browsed than their counterparts in the planted sub-variants. As a result, oaks in the planted pines were less affected by deer browsing and grew faster than oaks in the sown pine patches. This relation, however, existed only for variants 2 and 3. In variant 1, which had lower tree density, and solely individual oaks planted, the observed higher deer pressure (Borkowski et al. 2017) resulted in similar oak height regardless of the pine recruitment method (Fig. 4).

Factors affecting oak height at the individual oak/nest scale

The height of surrounding pines influenced the oak height also in the scale of individual saplings/nests. In contrast, the number of pine trees in the vicinity of the sapling/nest had no influence on the oak height in any of the variants. This is in accordance with our previous study (Borkowski et al. 2017), which demonstrated that the number of pine trees in the sapling/nest neighbourhood generally affected browsing on oak sapling less than did the pine height. The saplings/nests surrounded by taller pines were browsed significantly less than those surrounded by shorter pines. Pedunculate oak is a light-demanding species, but it can grow when surrounded by other trees if the main shoot is not shaded (Dobrowolska 2008). This was not the case, and thus, oak height in the present study was not negatively affected by the surrounding pines' height. Interestingly, the positive relation between the oak height and the pine height existed only in variants 2 and 3. In variant 1, where the browsing pressure was spread over a lower oak tree density and therefore was more intense per tree, the taller pines surrounding oak trees were not able to protect oaks.

Influence of within nest location on oak height

Oak location within the nests did not influence oak height. Our results were in agreement with other studies focused on nesting and browsing (Saha et al. 2012). It needs to be stressed that the oaks from the peripheral zone of the nests did not differ in height from the saplings growing in the more central zones, in spite of the higher deer browsing pressure exerted on them (peripheral oaks) (Borkowski et al. 2017). The intraspecific competition was probably a factor influencing the growth of the oaks. The saplings in the peripheral zone of a nest, having pines on one side, were probably under milder competition from the other oaks, while in the case of the oaks growing in the inner zones, the intraspecific competition was more pronounced.

Distribution of the tallest oak trees in the variants

The percentage of the tallest trees (> 150 cm) was much lower in variant 1 than in the other two variants. The difference was small between the other two variants. The number of the tallest trees per ha differed considerably between the variants: variant 1, 27; variant 2, 454; and variant 3, 483. Since the oak trees in variants 2 and 3 were planted in nests, both the total number of the most promising trees and their distribution among the nests were important. In approximately 40% of the nests, there were at least two promising trees (Table 4). Although chronic browsing in the Pisz Forest District was suppressing oak regeneration, the number of saplings taller than 150 cm seemed to be sufficient to create future stands. The experiment was undertaken in poor site types (coniferous site type) where Scots pine is recommended to be the main future tree with the share of auxiliary tree species being approximately 10% (Principles of silviculture 2012).

Conclusions

The current study provides insight into the discussion about the methods of establishing oak (and probably other deciduous tree species attractive to deer) admixtures in stands under the pressure of ungulates. This 10-year experiment has shown that artificial regeneration of oak can occur in an unfenced area with fairly high browsing pressure. Literally, all the oak trees in all variants were browsed each year for four consecutive years (Borkowski et al. 2017). Nevertheless, the effects of the browsing pressure on the oak growth were modified by both the inter- and intraspecific neighbourhoods. The interspecific neighbourhood referred to the characteristics of pine trees surrounding the oak saplings or nests. The effects of pines on oaks could be seen in all the spatial scales considered: plantation, pine recruitment method, and individual tree/nest scales. At all scales, taller pines reduced the browsing pressure, which enabled oak trees to grow faster. The effects of the browsing pressure were more apparent in the case of singly planted oaks, which were deprived of the presence of the intraspecific neighbourhood and simultaneously growing at the lowest density. The growth of the oak saplings planted in the higher densities (nests) was less affected by the deer browsing. There, a protective effect of the pine surroundings on oak height was found. In the low-nest density variant, the positive influence of the pine neighbourhood on the oak growth (pine regeneration method and individual sapling scales) was much milder than in variants with higher next density.

We demonstrated that the oaks planted in higher nest densities grew better than those in the lower-density treatment. Our results also suggested that there is room for optimising the number of oak nests. Our results did not support the original claim by Szymański (1977) that the interior oaks, due to the protective function of the peripheral oaks, should be superior within a nest. In our study, there were no substantial differences in oak growth based on their location within a nest. It needs to be remembered, however, that the oaks from the peripheral zone were under higher deer pressure than the internal oaks and that the lack of difference in their heights suggests that the peripheral oaks had a higher growth potential than the oaks located closer to a nest centre. Thus, in regions with frequent browsing, we recommend planting species selected by ungulates in high tree densities. Moreover, we restate our previous recommendation that more often browsing species be planted several years after the conifer species. This assures the conifer species can become established and can provide cover and facilitate the growth of the browsing species.

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References

Ackzell L (1993) A comparison of planting, sowing and natural regeneration for *Pinus sylvestris* (L.) in boreal Sweden. For Ecol Manag 61:229–245

Annighöfer P, Beckschafer P, Vor T, Ammer Ch (2015) Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl, *Quercus robur* L.) in dependence of environment and neighborhood. PLoS ONE 10(8):1–16

Bergquist J, Orlander G (1998) Browsing damage by roe deer on Norway spruce seedlings planted on clearcuts of different ages. 1. Effect of slash removal, vegetation development, and roe deer density. For Ecol Manag 105:283–293

Bergquist J, Orlander G, Nilsson U (2003) Interactions among forestry regeneration treatments, plant vigour and browsing by deer. New For 25:25–40

Bernadzki E, Bolibok L, Brzeziecki B, Zajaczkowski J, Zybura H (1998) Compositional dynamics of natural forests in the Bialowieza National Park, northeastern Poland. J Veg Sci 9:229–238

Bideau E, Maublanc ML, Picot D, Hamard JP, Ballon P, Gerard JF (2016) Short-term browsing by roe deer has little effect on survival and growth of sessile oak seedlings. Scand J For Res 31(1):40–45

Borkowski J, Palmer SCF, Borowski Z (2011) Drive counts as a method of estimating ungulate density in forests: mission impossible? Acta Theriol 56:23–235

Borkowski J, Dobrowolska D, Dąbrowski W, Banul R, Załuski D (2017) Young conifer stands form a deer browsing refuge for an oak admixture: silvicultural implications for forest regeneration under herbivore pressure. Eur J For Res 136:787–800

Bradfer-Lawrence T, Rao S (2012) Deadwood fencing used to protect broadleaved trees from deer browsing in the Cairngorms, Scotland. Conserv Evid 9:72–76

Canham ChD, McAninch JB, Wood DM (1994) Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. Can J For Res 24:817–825

Chaar H, Colin F, Leborgne G (1997) Artificial defoliation, decapitation of the terminal bud, and removal of the apical tip of the shoot in sessile oak seedlings and consequences on subsequent growth. Can J For Res 27:1614–1621

Cote SD, Rooney TP, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Ann Rev Ecol Evol Syst 35:113–147

Cutini A, Bongi P, Chianucci F, Pagon N, Grignolio S, Amorini E, Apollonio M (2011) Roe deer (*Capreolus capreolus* L.) browsing effects and use of chestnut and Turkey oak coppiced areas. Ann For Sci 68:667–674

Dobrowolska D (2008) Effect of stand density on oak regeneration in flood plain forests in Lower Silesia, Poland. Forestry 81:511–523

Dobrowolska D (2014) Forest regeneration in northeastern Poland following a catastrophic blowdown. Can J For Res 45(9):1172–1182

Drexhage M, Colin F (2003) Effects of browsing on shoots and roots of naturally regenerated sessile oak seedlings. Ann For Sci 60:173–178

Eiberle K (1975) Ergebnisse einer Simulation des Wildverbissesdurch den Triebschnitt. Schweiz Z Forstwes 126:821–839

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Ulmer, Stuttgart

Faison EK, DeStefano S, Foster DR, Motzkin G, Rapp JM (2016) Ungulate browsers promote herbaceous layer diversity in logged temperate forests. Ecol Evol 6:4591–4602

Farjon A (2005) Pines: drawings and descriptions of the genus *Pinus*, 2 revised edn. Brill, Leiden

Frost CJ, Hunter MD (2004) Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. Ecology 85:3335–3347

Gerhardt P, Arnold JA, Hackländer K, Hochbichler E (2013) Determinants of deer impact in European forests-a systematic literature analysis. For Ecol Manag 310:173–186

Gill RMA (2000) The impact of deer on woodland biodiversity. Forestry Commission

Götmark F, Kiffer C (2014) Regeneration of oaks (*Quercus robur*/*Q. petraea*) and threeother tree species during long-term succession after catastrophic disturbance (windthrow). Plant Ecol 215:1067–1080

Götmark F, Berglund Å, Wiklander K (2005) Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scand J For Res 20:223–234

Gussone HA, Richter A (1994) Eichen-Nester. Forst und Holz 49:300–304

Halpern SL, Underwood N (2006) Approaches for testing herbivore effects on plant population dynamics. J Appl Ecol 43:922–929

Harmer R (2001) The effect of plant competition and simulated summer browsing by deer on tree regeneration. J Appl Ecol 38:1094–1103

Hartley SE, Iason GR, Duncan AJ, Hitchcock D (1997) Feeding behaviour of Red Deer (*Cervus elaphus*) offered Sitka Spruce saplings (*Picea sitchensis*) grown under different light and nutrient regimes. Funct Ecol 11:348–357

Hegland SJ, Leleeng MS, Moe SR (2013) Old-growth forest floor richness increases with red deer herbivory intensity. For Ecol Manag 310:267–274

Hoogesteger J, Karlsson PS (1992) Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). Funct Ecol 6:317–323

Jensen AM, Götmark F, Löf M (2012) Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: a field experiment. For Ecol Manag 266:187–193

Jones BE, Lile DF, Tate KW (2009) Effect of simulated browsing on aspen regeneration: implications for restoration. Rang Ecol Manag 62:557–563

Kullberg Y, Bergström R (2001) Winter browsing by large herbivores on planted deciduous seedlings in southern Sweden. Scand J For Res 16:371–378

Kullberg Y, Welander NT (2003) Effects of simulated winter browsing and drought on growth of *Quercus robur* L. seedlings during establishment. For Ecol Manag 173:125–133

Kupferschmid A (2018) Selective browsing behaviour of ungulates influences the growth of Abies Alba differently depending on forest type. For Ecol Manag 429:317–326

Lorenc H (2005) Atlas of Polish climate. IMiGW, Warszawa **(in Polish)**

Lyly O, Saksa T (1992) The effect of stand density on moose damage in young *Pinus sylvestris* stands. Scand J For Res 7:393–403

Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. For Ecol Manag 88:93–98

Motta R (2003) Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. For Ecol Manag 181:139–150

Nahlik A, Walter-Illes W (1998) Die Einwirkung des Wildverbisses auf die Mortalität und das Höhenwachstum der Pflanzen verschiedener Baumarten—ein simuliertes Experiment. Beiträge zur Jagd- und Wildforschung 23:95–105

Pepin D, Renaud PC, Boscardin Y, Goulards M, Mallet C, Anglard F, Ballon P (2006) Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings—an enclosure-based experiment. For Ecol Manag 222:302–313

Price PW (1991a) Darwinian methodology and the theory of insect herbivore population dynamics. Ann Entomol Soc Am 84:465–473

Price PW (1991b) The plant vigour hypothesis and herbivore attack. Oikos 62:244–251

Principles of silviculture (2012) CILP, Warszawa, 72 pp **(in Polish)**

Reimoser S, Partl E, Reimoser F, Vospernik S (2009) Roe-deer habitat suitability and predisposition of forest to browsing damage in its dependence on forest growth-model sensitivity in an alpine forest region. Ecol Model 220:2231–2243

Report of Forest Status (2016) CILP, Warszawa **(in Polish)**

Saha S, Kuehne C, Kohnle U, Brang P, Ehring A, Geisel J, Leder B, Muth M, Petersen R, Peter J, Ruhmi W, Bauhus J (2012) Growth and quality of young oaks (*Quercus robur* and *Quercus petraea*) grown in cluster nest plantings in central Europe: a weighted meta-analysis. For Ecol Manag 283:106–118

Spathelf P, Ammer C (2015) Forest management of scots pine (*Pinus sylvestris* L.) in northern Germany-a brief review of the history and current trends. Forstarchiv 86(3):59–66

Szymański S (1966) Wzrost i morfologia dębu szypułkowego (*Quercus robur* L.) w uprawach gniazdowych i rzędowych powstałych z sadzenia [Growth and morphology of pedunculate oak planted in rows or nests]. Prace Kom Nauk Rol Kom Nauk Leś PTPN 22:1–74

Szymański S (1977) Zastosowanie gniazdowej metody uprawy dębu (wg Ogijewskiego) na bogatych siedliskach [Using of nest method for oak planting (according to Ogiejewski) on rich habitats]. Sylwan 121:43–54

TIBCO Software Inc. (2017) Statistica (data analysis software system), version 13. http://statistica.io

Van Hees FM, Kuiters LAT, Slim PA (1996) Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. For Ecol Manag 88:55–63

Ward AI, White PCL, Walker NJ, Critchley CH (2008) Conifer leader browsing by roe deer in English upland forests: effects of deer density and understorey vegetation. For Ecol Manag 256:1333–1338

Weinreich A, Grulke M (2001) Vergleich zwischen Nesterpflanzung und konventioneller 795 Begründung von Eichenbeständen. Freibr Forst Forsch 25:41–54

Zamora R, Gómez JM, Hódar JA, Castro J, García D (2003) Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. For Ecol Manag 144:33–42