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Abstract *(max 400 words)*

Coppice forestry is a conventional silvicultural practice that takes advantage of a tree's capacity to respond to disturbances by sprouting. Sprouting capacity is determined by many intrinsic and extrinsic factors such as parent tree age/size, understory light availability and deer browsing, which, under closed canopy conditions are important limiting factors for stump survival or sprout growth. However, the combined effect of potentially confounding abiotic and biotic factors on stump survival and sprout growth remains elusive, even more so under closed canopy conditions. This study aims to quantify the effect of deer browsing on stump mortality and sprout growth under closed-canopy conditions and to compare this effect with other known determinants. Here we show that stump survival and sprout growth in sessile oak (*Quercus petraea* Matt.) depend on deer browsing, understory light availability and the diameter of the parent tree. By studying paired fenced-unfenced plots, we confirmed that deer browsing decreased stump survival and inhibited sprout growth. Furthermore, by taking advantage of a gradient in understory light availability in monospecific and mixed stands of sessile oak and Scots pine (*Pinus sylvestris* L.), we showed a clear positive linear relationship between sprout growth and light availability. This relationship explained the observed differences among stand composition types. Finally, we found that increased understory light availability did not compensate for losses due to deer browsing. In the absence of deer browsing, our results demonstrate that sessile oak stumps regenerate well under closed-canopy conditions and maintain a moderate sprouting capacity at least until the age of 70-80 years old. Partial thinning could therefore be a potential tool to renew light-demanding tree species such as sessile oak in mixed high-forest stands. Nevertheless, we do not recommend coppicing sessile oak under closed canopies unless the oak stumps are protected from deer browsing and understory light availability is optimized as much as possible despite closed-canopy-management objectives.

Keywords *(max 6)*: Coppice, Deer impact, Ecological threshold, Mixed forest, *Quercus petraea*, *Pinus sylvestris*

1 Introduction

Deer populations have increased in numerous regions in the Northern Hemisphere (Apollonio *et al.*, 2010; Kaji *et al.*, 2010; Hewitt, 2011), where they have become locally overabundant. Several studies report damage to forest dynamics and biodiversity. For example, high browsing pressure has led to the biotic impoverishment and homogenization of forest understory plant communities (Rooney, 2009; Martin *et al.*, 2010; Boulanger *et al.*, 2018), and forest managers are finding it harder to regenerate the forest (Gill, 1992; Putman and Moore, 1998; Danell *et al.*, 2003; Tremblay *et al.*, 2007).

Silvicultural systems where trees regenerate vegetatively by producing stump sprouts and where the rotation is comparatively short are known as coppice forestry (Sjölund and Jump, 2013), and were once quite common in many parts of Western and Central Europe in lowland temperate broadleaf forests (Hédl *et al.*, 2010). In some parts of Europe, coppice forestry has recently been revived in response to demands for nature conservation and renewable energy (Rydberg, 2000; Sjölund and Jump, 2013). Classical forms of coppicing are based on clear felling at regular intervals, varying from 7 to 40 years (Müllerová *et al.*, 2016). Coppicing under closed canopy cover has also been traditionally used in mountain regions as a protection against soil erosion (Nocentini, 2009).

Recently, other forms of coppicing have been developed to take advantage of sprouting after thinning or partial cutting, this allows trees to regenerate under circumstances where the objectives are to maintain a closed canopy for conservation purposes and to preserve mixed tree species assemblages with minimal intervention (Götmark, 2013; Sjölund and Jump, 2013; Leonardsson and Götmark, 2015). In this context, coppicing is seen as a way to renew and preserve light-demanding tree species, such as oak, in association with more shade-tolerant tree species while maintaining a continuous cover of mixed forests. Oaks are of particular interest as they are known to have strong sprouting capacity and to maintain this ability well into old age (Del Tredici, 2001). The regeneration

of oaks in temperate forests is subject to much controversy among forest researchers and practitioners (Götmark, 2007; Dey *et al.*, 2012; Bobiec *et al.*, 2018). Several factors have been proposed to explain the regeneration failure of oaks such as low light levels associated with the competition with shade-tolerant undergrowth (Kelly, 2002; Oliver *et al.*, 2005), browsing by large herbivores (Buckley *et al.*, 1998; Kuiters and Slim, 2002; Götmark *et al.*, 2005) and large-scale disturbances (Bobiec *et al.*, 2011; Dey *et al.*, 2017).

Many tree species respond to disturbances by sprouting to develop secondary replacement trunks (*sensu* Del Tredici, 2001), thus rapidly regaining lost biomass and occupying space immediately after the disturbance (Bond and Midgley, 2001). The ability to sprout is fairly common among adult trees in all forest biomes (Vesk and Westoby, 2004) and plays an important role in driving forest dynamics (Van Bloem *et al.*, 2007; Dietze and Clark, 2008; Edenius *et al.*, 2011; Marzano *et al.*, 2012). The capacity of tree stumps to survive and sprout after cutting is influenced by multiple intrinsic and extrinsic factors including the age and size of the parent tree (Del Tredici, 2001; Weigel and Peng, 2002; Matula *et al.*, 2012; Splichalova *et al.*, 2012), harvesting parameters such as cutting height and season (Harrington, 1984; Xue *et al.*, 2013), the density of living residual trees and neighboring stumps (Matula *et al.*, 2012; Svatek and Matula, 2015), thinning intensity and understory light availability (Ducrey and Boisserie, 1992; O'Hara and Berrill, 2010) and damage by deer browsing or pathogens (Kay, 1993; Cooke and Lakhani, 1996; Pyttel *et al.*, 2013; Forrester *et al.*, 2014; Marcais and Desprez-Loustau, 2014). Most of these factors can be controlled by the forest manager in order to optimize sprouting response after thinning or partial cutting, but the outcomes are uncertain as results on sprouting responses are contradictory.

This is particularly true for the oak genus (*Quercus* sp.), where results diverge among studies. On the one-hand, several studies of oaks have revealed negative relationships between parent tree diameter and stump survival and sprout growth (Khan and Tripathi, 1986; Weigel and Peng, 2002;

Matula *et al.*, 2012; Splichalova *et al.*, 2012). On the other hand, other studies have found the opposite relationship (Xue *et al.*, 2013) or no relationship at all (Leonardsson and Götmark, 2015). Likewise, the effect of thinning intensity remains elusive. Thinning intensity affected stump survival and sprout growth for *Quercus nigra* L. (Gardiner and Helmig, 1997), whereas a study on *Quercus pagoda* Raf. found no or very little effect (Lockhart and Chambers, 2007). This indicates that sprouting responses are either species-specific or interact with other factors not controlled for in the studies, such as deer browsing, pathogens, competing understory vegetation or forest stand history.

The present study aimed to simultaneously take into account the presence of deer browsing, light availability and neighboring species (stand composition) to study sprout survival and growth, and to assess their magnitude. From a management point of view, the main goal of the study was to evaluate whether partial thinning and the subsequent regrowth from cut stumps could be a potential method of forest renewal for a light-demanding tree species, in this case sessile oak (*Quercus petraea* Matt.), in high forest stands subjected to light to moderate deer browsing pressure. The objectives of the study were two-fold:

1) First, we compared sessile oak stump mortality and sprout growth in the presence and absence of deer in mono-specific and mixed stands of sessile oak and Scots pine (*Pinus sylvestris* L.). We hypothesized a negative impact of deer browsing on stump survival and sprout growth (H1), and no effect of stand composition on these parameters (H2).

2) Second, we compared the explanatory power of deer browsing in relation to other intrinsic and extrinsic environmental factors potentially affecting stump mortality and sprout growth. We hypothesized that a large parent-tree diameter would increase stump mortality (H3), while increased light, small parent-tree diameters and low plant cover for neighboring vegetation would increase sprout growth (H4).

2 Materials and Methods

2.1 Study site and sampling design

The study took place in the center of France, in the Orleans National Forest (France, 47°49' N, 2°29' E) where elevation ranges from 107 m to 174 m above sea level. Throughout the forest, the soil is relatively poor and acidic with a sandy clay-loam texture, and is classified as a planosol (IUSS Working Group WRB, 2015). Superimposed layers of clay and sand lead to a temporary perched water table in winter, but the low soil water storage capacity reduces available water for plants in summer. The area has a temperate continental climate with an oceanic influence: mean annual temperature is 10.8 °C and mean annual rainfall is 729 mm based on 1981-2010 data from the SAFRAN and the ISBA analytical platforms provided by Météo-France (Durand *et al.*, 1993).

Roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) are the main large herbivores, while large predators are absent from the study area. Wild boar (*Sus scrofa* L.) is also present, but is not known to cause any damage to oak sprouts, nor did we observe any damage that could be attributed to wild boar browsing during the study period. During the 2013/2014 hunting season, hunters killed on average 1.5 roe and 2.0 red deer individuals per square kilometer, indicating that the population densities of roe and red deer are low to moderate (Supplementary Figure 1). The study sites were equipped with camera traps (Moultrie 80XT) that were used to estimate local site use (hereafter 'local density') (Supplementary Figure 1). The estimated local density integrates habitat use and is not be confused with estimated absolute population density, as the camera traps were set up in particular forest habitats and not randomly throughout the home range of the deer population. We used a random encounter model (REM) to estimate local densities (Rowcliffe *et al.*, 2008; Lucas *et al.*, 2015). The average local density at the study plots was estimated as 0.041±0.013 (mean ± SE; n=6) and 0.11±0.032 (n=6) individuals per square kilometer for red and roe deer, respectively. The large discrepancy between these estimates of local densities and the hunting

statistics is mainly due to habitat selection. Our study plots were situated in mature forest stands with relatively sparse understory vegetation. These habitats are often avoided by deer, who prefer young dense forest stands, forest edges or open habitats (Latham *et al.*, 1996).

Six sites with paired fenced-unfenced 0.5-ha plots were set up in stands of sessile oak and Scots pine in the framework of the OPTMix experiment (Korboulewsky *et al.*, 2015). Fences were erected in the winter of 2013/2014 to exclude large wild ungulates; the fences are approximately 2.0 m tall with a mesh size of about 15 cm. Our selected stands were even-aged stands between 70 and 80 years old with a dominant height of between 18 and 21 m for oaks and between 19 and 24 m for pines. The 12 plots, including the buffer zone (20 m wide), are all being managed under the same silvicultural treatments and they have similar forest stand characteristics (Table 1). The stands are relatively low density as a result of a dynamic management strategy which allows for understory regrowth from coppice stumps, similar to a coppice-with-standards (CWS) silvicultural system. The CWS system is composed of a two-story forest structure with a coppice understory and scattered taller single-stemmed trees as an overstory (Sjölund and Jump, 2013).

Table 1. Stand characteristics in 2015 of the paired fenced-unfenced study plots in even-aged mono-specific stands of sessile oak (*Quercus petraea* Matt.) and Scots pine (*Pinus sylvestris* L.), and in even-aged mixed stands of sessile oak and Scots pine at the six study sites (O12, O214,O57, O216, O83, O200). N = number of stems per hectare; G = basal area per hectare at 1.3 m height; DBH = diameter at 1.3 m height; $PACL_{OBS}$ = percentage of observed above-canopy light at five random spots and at 2 m in height

	Oak		Mixed		Pine	
	O12	O214	O57	O216	O83	O200
Unfenced						
N_{oak} (stems/ha)	392	370	252	215	-	-
G_{oak} (m^2/ha)	14.5	14.7	9.9	8.1	-	-
DBH_{oak} (cm)	20.9 (6.0)	21.7 (5.8)	21.1 (7.4)	21.1 (5.9)	-	-

N_{pine} (ind/ha)	-	-	86	112	290	200
G_{pine} (m^2/ha)	-	-	10.6	9.3	25.4	19.5
DBH_{pine} (cm)	-	-	39.2 (6.1)	31.8 (6.1)	32.9 (5.5)	34.9 (4.9)
$PACL_{OBS}$ (%)	21.4 (2.6)	19.8 (2.2)	29.8 (3.6)	30.2 (4.0)	36.3 (1.9)	34.3 (7.8)
Fenced						
N_{oak} (ind/ha)	354	294	194	170	-	-
G_{oak} (m^2/ha)	15.3	14.0	8.5	7.1	-	-
DBH_{oak} (cm)	22.6 (6.3)	24.0 (5.6)	22.5 (7.3)	21.8 (7.8)	-	-
N_{pine} (ind/ha)	-	-	94	116	239	202
G_{pine} (m^2/ha)	-	-	11.7	9.8	24.6	19.4
DBH_{pine} (cm)	-	-	39.3 (6.6)	32.0 (7.5)	35.8 (5.3)	34.7 (4.4)
$PACL_{OBS}$ (%)	20.7 (3.7)	17.2 (4.2)	28.8 (4.8)	28.4 (3.9)	35.1 (4.2)	33.4 (1.7)

2.2 Stump mortality and sprout growth

The study plots were thinned during the 2012-2013 and 2013-2014 winter seasons (Table 2) in order to reach targeted stand tree composition (monospecific and mixed stands) and densities (low density). Cut stems were monitored in March 2015 and 2016, just before the start of the plant growing season. A stump was considered dead if it had no living buds or shoots at the time of the inventories. For all living stumps, the vertical height of the tallest shoot was measured as well as the length of the five most vigorous shoots. Vertical shoot height was defined as the vertical distance between the ground and the tip of the shoot and shoot length was defined as the distance following the curvature of the stem from the base to the tip of the shoot. The five most vigorous shoots were tagged in 2015 and re-measured in 2016. Sprout growth in the 2015 growing season was estimated by calculating the difference in height/length of the shoots between the two measuring campaigns; this figure was used in subsequent analyses on sprout growth capacity. Signs of deer browsing (twigs showing a ragged tear or splintered cut on one side) and fraying (bark rubbed off by the antlers) or other types of damages by rodents (twigs showing sharp and inclined scissor-like cuts, bark gnaws and peeling), gall formations (abnormal outgrowths), plant tissue losses due to insect herbivory (ragged leaf edges, leaves perforated, skeletonization, leaf mining patterns), fungal attacks

190 (discoloration, wilting, fruiting bodies), climatic events (dead tissue, wilting) and damage of other
191 origins were recorded at the stump level.
192
193 In all, 301 oak stumps were monitored for two years (2015 and 2016) of which 148 (49.2%) were still
194 alive at the end of the study. All stumps in the pure oak stands originated from single-stemmed
195 parent trees, while 15-20% of the stumps in the pure pine and mixed stands originated from multi-
196 stemmed parent trees. Multi-stemmed parent trees likely originated from former coppices, contrary
197 to the single-stemmed parent trees which probably grew from seeds through natural regeneration or
198 had been planted as seedlings. Furthermore, all the parent trees in the pure pine stands were
199 subordinate oak trees before thinning, whereas in the mixed pine / oak and pure oak stands,
200 respectively 92-96% and 75-77% of the parent trees were subordinate. Six hundred and sixty-six
201 shoots were tagged in 2015, of which 563 shoots were re-measured in 2016 to calculate annual
202 growth in length. The other 103 shoots had died. The overall average DBH_{parent} of cut trees was 15.9
203 cm (SD = 4.7 cm, range 7-25.2 cm, n = 301).
204
205 Table 2. Date of thinning events and the number of oak stumps monitored at the six study sites in the
206 paired fenced-unfenced 0.5-ha plots

	Oak		Mixed		Pine	
	O12	O214	O57	O216	O83	O200
Thinning						
Date	Dec 2012	Jan 2013	Dec 2012	Nov 2013	Nov 2013	Feb 2014
Number of oak stumps						
Unfenced	29	30	27	30	16	21
Fenced	30	30	21	30	16	21

207

208 ## 2.3 Covariates

209 For each of the 12 plots, all trees with a diameter above 7.5 cm DBH were inventoried and mapped
210 before and after thinning. We used diameter at breast height of the parent tree (DBH_{parent}) as a
211 potential explanatory variable and as a proxy for tree size.

Understory light availability at oak stump locations was estimated by a model based on the Beer-Lambert law, which predicts from data on basal area the percent of above-canopy light (PACL) that reaches the understory vegetation (Sonohat *et al.*, 2004; Balandier *et al.*, 2006). The model had been calibrated for mono-specific and mixed stands of sessile oak and Scots pine and its predictive ability evaluated for the plots concerned (see Perot *et al.*, 2017). As proposed by Perot et al. (2017), a single model was applied to both mono-specific and mixed stands as follows:

$$PACL_i = e^{(-b_{oak}G_{oak} - b_{pine}G_{pine})} + \varepsilon_i$$

where $PACL_i$ is the percent of above-canopy light at point *i*, *G* is the local basal area per hectare at point *i*, *b* is the coefficient of extinction and ε_i is the residual part of the model. Parameters and variables associated to sessile oak are annotated with the *oak* index and those associated with Scots pine are annotated with the *pine* index. PACL is defined as the ratio between below-canopy and above-canopy photosynthetically active radiation (PAR), which is the equivalent of the solar radiation transmittance of the tree canopy. Model predictions of PACL are hereafter referred to as $PACL_{EST}$.

Competition with the surrounding vegetation was determined within a radius of two meters centered on the stumps by visually estimating the vertical projection of plant cover of the most common and most dominant understory plant species (*Molinia caerulea* L., *Calluna vulgaris* L., *Pteridium aquilinum* L., *Rubus fruticosus* agg. L.). Seven classes were used: absence, cover <1%; 1% < cover < 5%; 5% < cover < 20%; 20% < cover < 50%; 50% < cover < 75%; and 75% < cover < 100%. We pooled the cover data before all subsequent analyses and assumed the independence of the spatial distribution of plant individuals. We applied the method developed by Fischer (2015) to estimate overall plant cover for the understory vegetation layer. The pooled plant cover was bounded between 0-100%.

2.4 Statistical analyses

Generalized mixed effects models (GLMM) were used to test the effect of deer browsing and stand composition on oak stump mortality and sprout growth capacity. A random intercept model was fitted as reference model to test for differences related to the experimental design, where stand composition and herbivore exclusion and their interaction were fixed terms. For analyses at the stump level, the random terms were composed of site and study plot nested within site in order to take into account the nested sampling design of paired fenced-unfenced plots. For analyses at the shoot level, stump was added as an additional random effect nested within plot. Then, in order to see whether DBH_{parent}, $PACL_{EST}$ and plant cover of competing vegetation–potential covariates–improved model fitting or could replace one of the fixed terms in the reference model, they were added to the model which was then compared to the reference model. Finally, a minimal adequate model was selected corresponding to the most parsimonious model. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc) (Burnham and Anderson, 1998). When the difference between the minimum AICc value and the AICc values of the other possible models was less than 2, we judged the models to be of equivalent explanatory power and retained the most parsimonious one.

We used the maximum likelihood (ML) estimation method to compare and fit the models because we were comparing models that had different fixed effects (Pinheiro and Bates, 2000). The final selected models were fitted with the restricted maximum likelihood (REML) method in order to better estimate the variance components (Pinheiro and Bates, 2000). Model efficiency (EF), which can be used as a proxy for the proportion of variation explained in non-linear models (Mayer and Butler, 1993), was calculated as follows:

$$EF = 1 - \frac{\sum(y_{i-}\hat{y}_i)^2}{\sum(y_{i-}\bar{y})^2}$$

where y_i is the observed value, $\hat{y}_i$ is the fitted value and $\bar{y}$ is the mean of the observed values. *EF* was computed both with and without random effects, which allowed us to evaluate the proportions explained by the fixed and the random part of the model.

For stump mortality, which is a binary variable (dead or alive), we used a binomial error distribution. For shoot growth, which is a continuous variable, we used a normal error distribution. Statistical analyses were performed with the R software, version 3.1.0 (R Development Core Team, 2011). Mixed effects models were run with the glmer function of the lme4 package for data with a binomial error distribution (Bates *et al.*, 2014) and with the lme function of the nlme package for data with a normal error distribution (Pinheiro *et al.*, 2011).

3 Results

3.1 Stump survival

Oak stump survival after 2-3 growing seasons in late winter 2016 was on average 1.6 times higher in fenced than in unfenced plots (Figure 1). Adding DBH_{parent} enhanced model predictions (Table 3) and showed a negative linear correlation between survival rate and DBH_{parent} (Figure 2). Although stand composition and its interaction with herbivory were not retained in our most parsimonious model, we observed a lower survival rate (P_{oak}=0.03 and P_{pine}=0.02) of oak stumps inside fenced plots in mixed oak-pine stands (see Supplementary Figure 3).

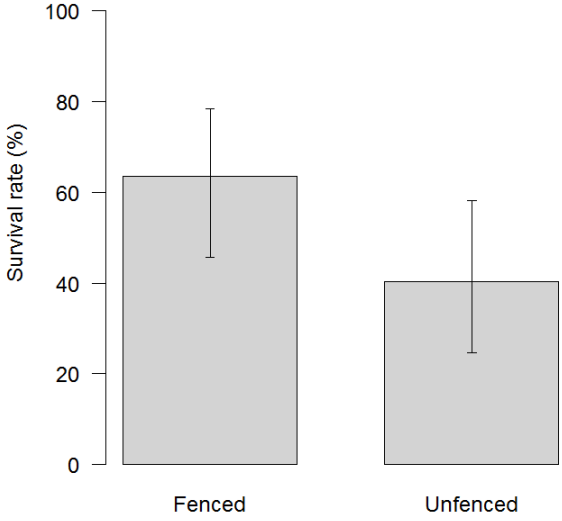


Figure 1. Survival rate of oak stumps in late winter 2016 in fenced and unfenced plots. Values correspond to the predictions of the most parsimonious model (Table 3) and error bars represent the 95% confidence interval around the model predictions, without taking random effects into account.

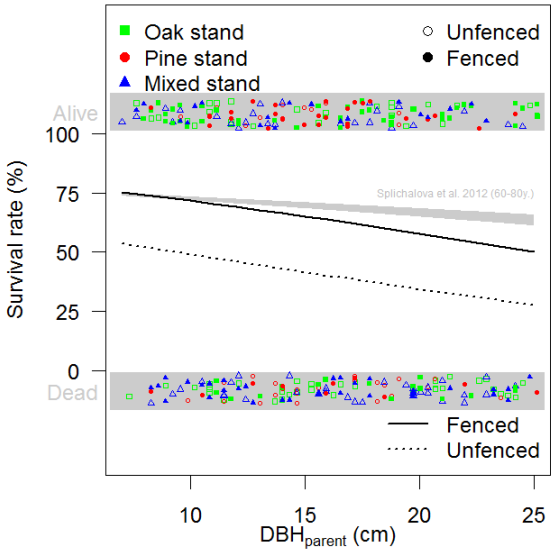


Figure 2. Observed survival (alive or dead) in 2016 of 301 oak stumps in relation to the diameter at breast height of the parent tree, DBH_{parent}, as well as the predicted survival rates for stumps in fenced (solid line) and unfenced (dotted line) plots taken from the most parsimonious $GLMM_{binom}$. For comparison, the results obtained by Splichalova *et al*. (2012) for equivalent tree ages and diameters are shown as a shaded gray interval.

Table 3. Summary of the statistics for the models predicting the survival rate (SURV) of sessile oak stumps in mono-specific and mixed sessile oak/Scots pine stands

Model[§]	N	df	σ_{site}	σ_{plot}	AICc	EF_{full}	EF_{fix}
Null model							
SURV = INTERCEPT	301	3	<0.001	0.80	399.4	0.16	-
Reference model (experimental design)							
SURV = C + H + C × H	301	8	0.32	<0.001	396.5	0.15	0.10
SURV = H	**301**	**4**	**0.37**	**0.21**	**397.8**	**0.16**	**0.037**
Diameter at breast height of the parent tree (DBH_{parent}) as covariate							
SURV = C + H + C × H + DBH_{parent}	301	9	0.30	<0.001	393.1	0.17	0.12
SURV = C + H + C × H + DBH_{parent} + H × DBH_{parent}	301	10	0.31	<0.001	394.2	0.17	0.12
SURV = H + DBH_{parent}	**301**	**5**	**0.19**	**0.42**	**394.6**	**0.18**	**0.051**

[§]A first model was fitted that tested for differences related to the experimental design (reference model), where stand composition (C), herbivore exclusion (H) and their interaction were fitted as fixed terms. The random term was composed of site and study plot nested within site in order to take into account the nested sampling design (paired fenced-unfenced plots). DBH_{parent} was added as a covariate (including interaction terms) in order to see whether this variable improved model fitting or could replace one of the fixed terms in the first model. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc). Only the best models, with a difference in AICc of less than 2, are displayed. The most parsimonious models are shown in bold.

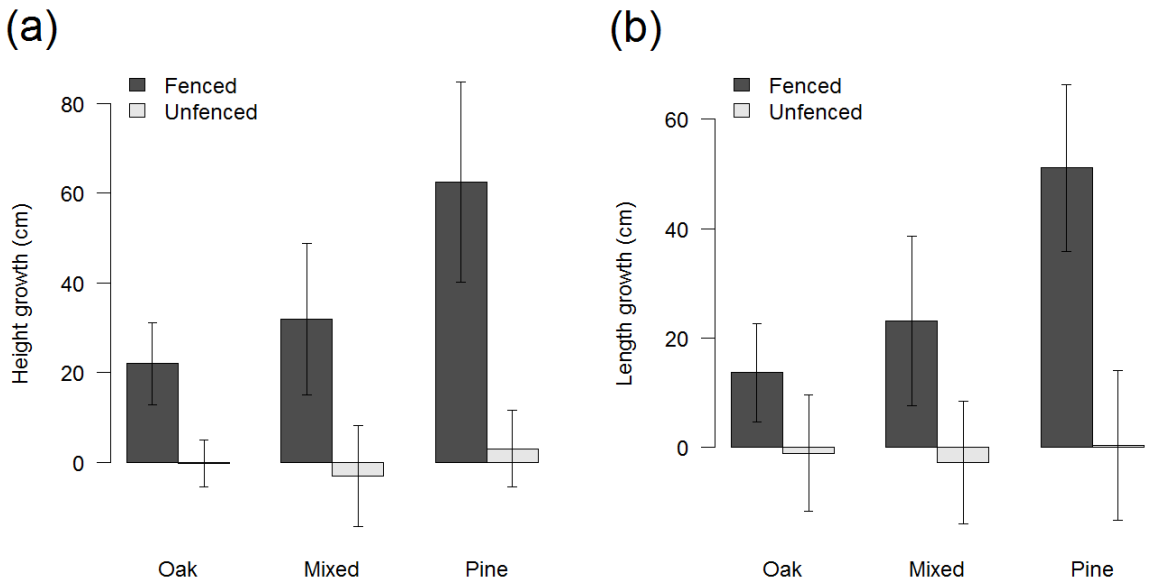
3.2 Sprout growth

The annual maximum height growth on oak stumps was greater in fenced than in unfenced plots (Figure 3a), the latter showing on average an annual height growth equal to zero in all stand compositions (Figure 3a). In fenced plots, sprout growth differed among stand compositions (Table 4). Growth tended to be the strongest for oak stumps in mono-specific pine stands (mean ± CI; 62.5±22.3 cm), intermediate in mixed oak-pine stands (31.8±16.9 cm) and the weakest in mono-

309 specific oak stands (22.0±9.1 cm). The annual growth in length of the five most vigorous shoots per

310 stump showed a similar pattern (Figure 3b).

311



312

313 Figure 3. Predicted annual growth in (a) sprout height and (b) length of the five most vigorous shoots

314 from oak stumps during the 2015 growing season in fenced and unfenced plots in mono-specific and

315 mixed sessile oak/Scots pine stands. Error bars represent the 95% confidence interval around the

316 model predictions.

317

318 Further, we found that annual height growth of shoots from oak stumps was equally well explained

319 by a model where composition was replaced by $PACL_{EST}$ (percent of above-canopy light). Although

320 the model with $PACL_{EST}$ had a slightly higher AICc (Δ = 0.61) than the model with composition and

321 explained less of the variability (49% versus 51%) (Table 4), we gained in model simplicity. That is, the

322 model had fewer parameters because a continuous variable replaced a categorical variable with

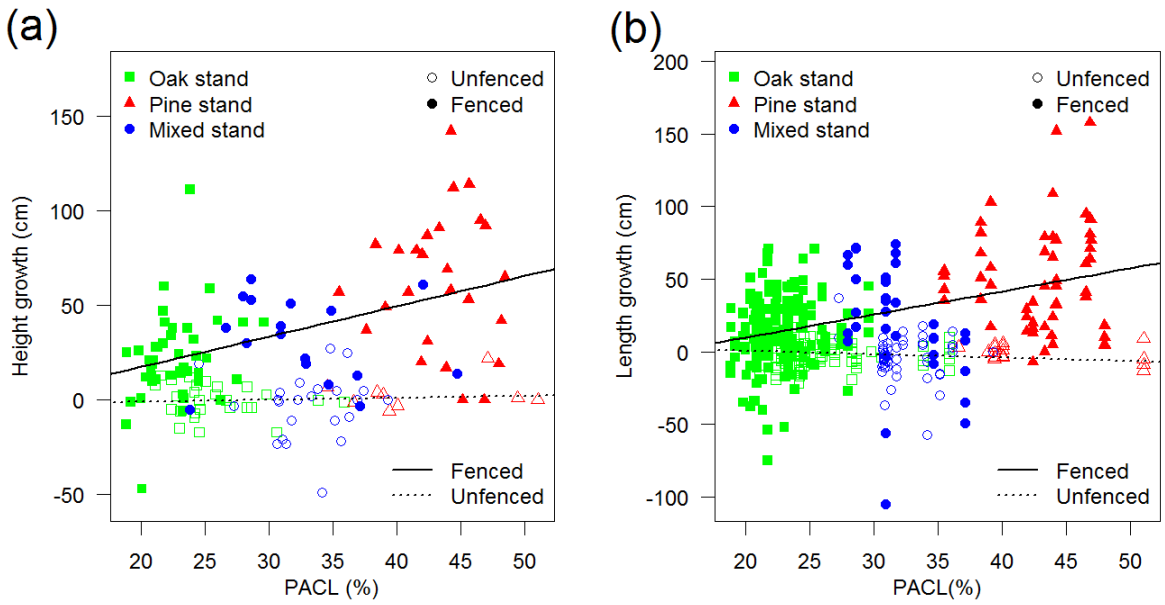
323 three levels. Indeed, $PACL_{EST}$ differed at stump locations among stand compositions (Figure 4).

324 $PACL_{EST}$ was the greatest for stumps in pine stands (mean = 43%, min = 35%, max = 51%, SD = 4.1%, n

325 = 35), intermediate in mixed stands (mean = 33%, min = 24%, max = 45%, SD = 4.4%, n = 57) and the

326 least in oak stands (mean = 24%, min = 19%, max = 36%, SD = 3.3%, n = 71). In fenced plots, the

327 model predicted a 14.4 cm increase in annual height growth for every 10% increase in $PACL_{EST}$, while
328 in unfenced plots the growth was not significantly different from zero irrespective of $PACL_{EST}$ (Figure
329 4).
330
331 Adding DBH_{parent} or total plant cover as covariates did not improve model fitting for either annual
332 sprout growth in height or annual growth in length of the five most vigorous shoots from oak stumps
333 (Table 4 and Supplementary Table 1).
334



335
336 Figure 4. Observed annual growth in (a) sprout height and (b) length of the five most vigorous shoots
337 from oak stumps during the 2015 growing season in fenced and unfenced plots in mono-specific and
338 mixed sessile oak/Scots pine stands in relation to the percent of above-canopy light ($PACL_{EST}$).
339 $GLMM_{normal}$ model predictions for shoots in fenced (solid line) and unfenced (dotted line) plots are
340 displayed.
341
342 Table 4. Summary of statistics for the models predicting annual height growth (HEIGHT) of sprouts on
343 sessile oak stumps in mono-specific and mixed sessile oak/Scots pine stands

Model[§]	N	df	σ_{site}	σ_{plot}	$\sigma_{resid.}$	AICc	EF_{full}	EF_{fix}

Null model								
HEIGHT = INTERCEPT	301	4	<0.001	554.5	507.2	1355.7	0.54	
Reference model (experimental design)								
HEIGHT = C + H + C × H	**301**	**14**	**<0.001**	**<0.001**	**541.0**	**1291.6**	**0.51**	**0.51**
Diameter at breast height of the parent tree (DBH_{parent}) as covariate								
HEIGHT = C + H + C × H + DBH_{parent}	**301**	**15**	**<0.001**	**<0.001**	**540.4**	**1294.1**	**0.51**	**0.51**
HEIGHT = C + H + C × H + DBH_{parent} + H × DBH_{parent}	301	16	<0.001	<0.001	534.4	1295.5	0.51	0.51
Percentage of above-canopy light ($PACL_{EST}$) as covariate								
HEIGHT = H + $PACL_{EST}$ + H × $PACL_{EST}$	**301**	**12**	**<0.001**	**<0.001**	**503.1**	**1292.2**	**0.49**	**0.49**
HEIGHT = C + H + $PACL_{EST}$ + H × $PACL_{EST}$	301	14	<0.001	<0.001	506.6	1293.4	0.50	0.50
Total plant cover ($COVER_{TOT}$) as covariate								
HEIGHT = C + H + C × H + $COVER_{TOT}$	**301**	**15**	**<0.001**	**<0.001**	**543.0**	**1294.0**	**0.51**	**0.51**
HEIGHT = C + H + C × H + $COVER_{TOT}$ + H × $COVER_{TOT}$	301	16	<0.001	<0.001	533.6	1295.8	0.51	0.51
HEIGHT = C + H + C × H + $COVER_{TOT}$ + C × $COVER_{TOT}$	301	17	<0.001	<0.001	545.7	1295.8	0.51	0.51

[§]A first model was fitted to test for differences related to the experimental design (reference model), where stand composition (C), herbivore exclusion (H) and their interaction were fixed terms. The random term was composed of site and study plot nested within site in order to take into account the nested sampling design (paired fenced-unfenced plots). Covariates were added to the model to see whether they improved model fitting or could replace one of the fixed terms in the first model. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc). Only the best models with a difference in AICc of less than 2 are displayed. The most parsimonious models are shown in bold.

3.3 Shoot damage

All the stumps (100%) in the unfenced plots were browsed by deer and showed few signs of other types of damage (13.0% in 2015 and 4.1% in 2016). Although no browsing by deer was observed inside fenced plots, damage did occur: in 2015 and 2016, respectively, only 16.3% and 6.9 % of stumps and 49.1% and 66.2% of tagged shoots were undamaged in the fenced plots. Some damage in the fenced plots was unidentified but we were able to determine most causes: powdery mildew attacks ($36.9\%_{2015}$ and $21.6\%_{2016}$, though frost damage could not be excluded as plausible alternative

cause), browsing by hares and small rodents (<1%$_{2015}$ and 4.0%$_{2016}$), and parasitic damage mostly due to gall formation and plant tissue losses through insect herbivory (<1%). Competing vegetation hindered growth for less than <1% of shoots in 2015and 3.1% in 2016. Oak shoots in pure pine stands had less damage in 2015 (corresponding to the 2014 growing season) than the shoots in monospecific oak and mixed stands (Supplementary Figure 2). Powdery mildew attacks (or possibly frost damage) were less common in pine stands during the entire study period and less common in mixed stands in 2016 (corresponding to the 2015 growing season) (Supplementary Figure 2b). An increase in damage caused by rodents and lagomorphs as well as hindered growth by vegetation competition was observed in monospecific pine and mixed stands in 2016 (Supplementary Figure 2c,d). Some parasitic attacks on oak shoots in monospecific oak stands were also observed in 2016, but not in monospecific pine and mixed stands. Finally, concerning repeated seasonal damage, in unfenced plots, the shoots tagged in 2015 that were found dead in 2016 had all but one been browsed at the time of measurement during previous growing season (65 shoots). In fenced plots, three quarters of the dead shoots had shown signs of damage by powdery mildew/frost (61%) and to a lesser extent by rodent/lagomorph browsing (11%) during the previous growing season; one quarter of the dead shoots had shown no signs of damage when measurements were taken during the previous growing season.

4 Discussion

We examined the effect of deer browsing on oak stump survival and sprout growth capacity. In accordance with H1, deer browsing negatively affected both the survival and growth of stump sprouts. However, contrary to H2, oak sprout growth differed among the three stand composition types (mono-specific and mixed oak/pine stands). In agreement with H4, we showed that these differences were partly due to differences in understory light availability among stand composition types. Contrary to H4, we found no effect on growth of total competing vegetation cover or diameter

383 at breast height of the parent tree (DBH_{parent}). Although DBH_{parent} had no effect on sprout growth, it
384 did have a relatively strong negative effect on stump survival, in agreement with H3.
385

386 4.1 Effects of deer browsing

387 Oak stumps experienced high browsing pressure: all the stumps in the unfenced plots were browsed
388 despite low to moderate deer population densities. Taking into account data from the camera trap
389 survey, local densities could even be considered very low. The high browsing pressure observed was
390 probably due palatability; stump sprouts are highly-preferred browse for deer, more than shoots
391 from seedlings and saplings that originate from seeds (Moore and Johnson, 1967). Consequently, and
392 in agreement with previous studies (Cooke and Lakhani, 1996; Espelta *et al.*, 2006; Cutini *et al.*, 2011;
393 Pyttel *et al.*, 2013; Forrester *et al.*, 2014; Royo *et al.*, 2016), we showed that deer browsing reduced
394 the height growth of oak stump shoots. Although stump sprouts are highly resilient to herbivory due
395 to their carbohydrate reserves (Bond and Midgley, 2001; Nzunda *et al.*, 2014), we showed that
396 sprout growth can still be totally inhibited. The mean maximum sprout height only reached the lower
397 limit of the browsing zone ('molar zone'; 0.2-1.8 m; Waller and Alverson, 1997; Frerker *et al.*, 2013).
398 In a short-term perspective, this is in line with the 'browsing lawn' concept (Cromsigt and Kuijper,
399 2011), in which intense browsing leads to increased resource availability (leaves and shoots within
400 the browsing height) and a proportional increase of palatable resources (oak sprouts) in the patch.
401 However, in a long-term perspective, it is likely that the positive effect of the immediate increase in
402 palatable food resources due to browsing will quickly fade away as stump mortality caused by the
403 same browsing increases (see below). Likewise, Cooke and Lakhani (1996) showed that ash sprouts
404 ceased to grow in height in unfenced areas that experienced high browsing pressure by muntjac
405 deer. However, forage preferences vary with tree species, and deer densities can differ greatly
406 among sites. This means that browsing pressure on sprouts can vary widely among forest areas (Royo
407 *et al.*, 2016). In other studies, the effect of deer browsing was less important, or even negligible, for
408 less palatable tree species than oak or in areas with apparently low deer population densities (Cutini

409 *et al.*, 2011; Royo *et al.*, 2016). These findings corroborate the idea that deer population densities do
410 not linearly translate into equivalent deer browsing impacts. Rather, they suggest that browsing
411 impact is context-dependent and depends on many factors other than deer density alone.
412
413 In line with the results obtained by Pyttel et al. (2013), we observed that oak stump mortality was
414 higher in unfenced plots. Probably the high browsing pressure on shoots and the repeated
415 consumption of sprouts in the unfenced areas increased stump mortality, similarly to what has been
416 shown for shrubs sprouting from below-ground organs (Moreno and Oechel, 1991). It is therefore
417 likely that repeated deer browsing depletes the plant's stored reserves (Paula and Ojeda, 2011;
418 Schutz *et al.*, 2011) and subsequently causes the plant to die (Canadell and Lopez-Soria, 1998). Royo
419 et al. (2016), on the other hand, found no relationship between deer browsing and tree stump
420 sprouting probability. None of the tested covariates or the correlations among covariates was able to
421 explain the difference in survival rate we found between mixed and mono-specific stands. Most
422 likely, the higher mortality in fenced mixed stands was due to higher attack rates of powdery mildew
423 (Supplementary Figure 2). Here it seems as if the oak stumps in pure pine stands benefited from the
424 absence of adult oak trees in the canopy which could be a local contamination source; much fewer
425 powdery mildew attacks were observed in pure pine stands. Powdery mildew infections are known
426 to be particularly severe on oak coppicing, but also to be present in mature trees where it is an
427 aggravating factor after insect defoliation (Marcais and Desprez-Loustau, 2014). It is also possible
428 that the observed lower survival rates were due to unknown differences in forest stand history such
429 as ancient forest fires or previous coppice treatments. However, we would then have expected a
430 lower survival rate in both the fenced and unfenced plots in the mixed stands, which was not the
431 case. Indeed, the survival rate in the unfenced mixed plots and the unfenced pure stands was similar
432 to the low rate in fenced mixed plots. Unknown covariates such as belowground interactions,
433 including competitive interactions, and fungal infections could also account for the observed
434 differences.

4.2 Effects of understory light availability

The quantity of light that reaches the forest floor is a strong determinant of growth, density and species composition of trees, shrubs and herbaceous plants under closed canopy conditions (Kobe *et al.*, 1995; Decocq *et al.*, 2004; Bartels and Chen, 2010). Not surprisingly, we found a positive linear relationship between understory light availability and sprout height growth for oak stumps protected from deer in the fenced plots. This is in agreement with other studies on oak stumps that have found shoot height growth to be higher in heavily thinned stands than in lightly thinned ones (Ducrey and Boisserie, 1992; Gardiner and Helmig, 1997). However, Lockhart and Chambers (2007) did not find any significant differences between lightly and heavily thinned stands. In our unfenced plots, we found that high understory light availability did not compensate for the impacts of deer browsing. Height growth was nil irrespective of light levels, even at the highest observed light availability. We believe that this was due to repeated browsing of shoots, which constantly kept them at the lower limit of the browsing zone.

4.3 Effects of diameter at breast height of the parent tree

Tree age and size is a strong determinant of forest dynamics; inequalities in tree size affect tree responses to disturbances (Merlin *et al.*, 2015), competitive interactions among neighbors (Cordonnier and Kunstler, 2015) and productivity (Bourdier *et al.*, 2016). We showed that stump mortality increased with increasing size of the parent tree (DBH_{parent}). These results are in line with North American (Dey and Jensen, 2002; Weigel and Peng, 2002; Sands and Abrams, 2009) and other European (Matula *et al.*, 2012; Splichalova *et al.*, 2012) studies of oak species. The predicted decrease in stump survival between the smallest and the largest trees in our sample set (25.1%) was equivalent to the observed drop in stump survival between fenced and unfenced plots (23.2%). From a management perspective, these results imply that the sprouting probability is acceptable for small

sessile oak trees in the absence of deer browsing, while sprouting is unacceptably low for larger trees in the presence of deer browsing. Compared to other European tree species, the survival rate of sessile oak stumps seems to be intermediate, lying between strongly-sprouting tree species such as the small-leaved lime (*Tilia cordata* Mill.) and European hornbeam (*Carpinus betulus* L.), and weakly-sprouting tree species such as silver and downy birch (*Betula pendula* L. and *B. pubescens* L.) and European beech (*Fagus sylvatica* L.) (Rydberg, 2000; Matula *et al.*, 2012; Leonardsson and Götmark, 2015).

5 Conclusion

Our results show that deer browsing was the most important determinant of sprouting capacity with strong effects on both stump survival and sprout growth. Diameter at breast height of the parent tree (DBH_{parent}, a proxy for tree size) was as important as deer browsing with regard to stump survival. For sprout growth, understory light availability was of lesser importance than deer browsing. We confirmed the results of other studies that deer browsing increases stump mortality and can even totally inhibit the height growth of coppice shoots under closed-canopy conditions, even at low deer population densities. We conclude that deer browsing is an important factor potentially responsible for explaining vegetative regeneration failures of oaks in temperate forests and forest managers should therefore carefully consider the presence of deer when coppicing is the desired management system. Furthermore, we do not recommend coppicing under closed canopy cover as a silvicultural practice unless stumps are protected from deer browsing. Even at relatively high light availabilities (PACL = 50%) corresponding to relatively large canopy openings, light was not sufficient to compensate for the losses due to deer browsing.

We also showed that understory light availability is a determinant for sprout growth, but that it did not seem to have any major effect on stump survival. On the other hand, DBH_{parent} did have a

relatively strong negative effect on stump survival, though our results confirm that sessile oak maintains an acceptably sprouting capacity into older age in the absence of deer browsing. These results imply that partial thinning could be useful to renew sessile oak under closed canopy conditions and to preserve light-demanding tree species in association with more shade-tolerant tree species in mixed high-forest stands. However, one should interpret our results cautiously as our study only spans two to three growing seasons, and does not take into consideration the long-term survival of re-sprouts under closed canopy conditions.

Additionally, we showed that the effect of a covariate (in our case PACL) on a response variable (sprout growth) might depend on another explanatory variable (deer browsing). These kinds of interactions may explain why some previous studies have found contradictory results. More specifically, in our study, browsing pressure cancelled or neutralized the effect of understory light availability ($PACL_{EST}$) and might explain some previous results related to the effect of thinning intensity. We therefore recommend that confounding factors be carefully taken into account and that deer browsing should systematically be controlled for in the experimental design of future studies on tree re-sprouting capacity.

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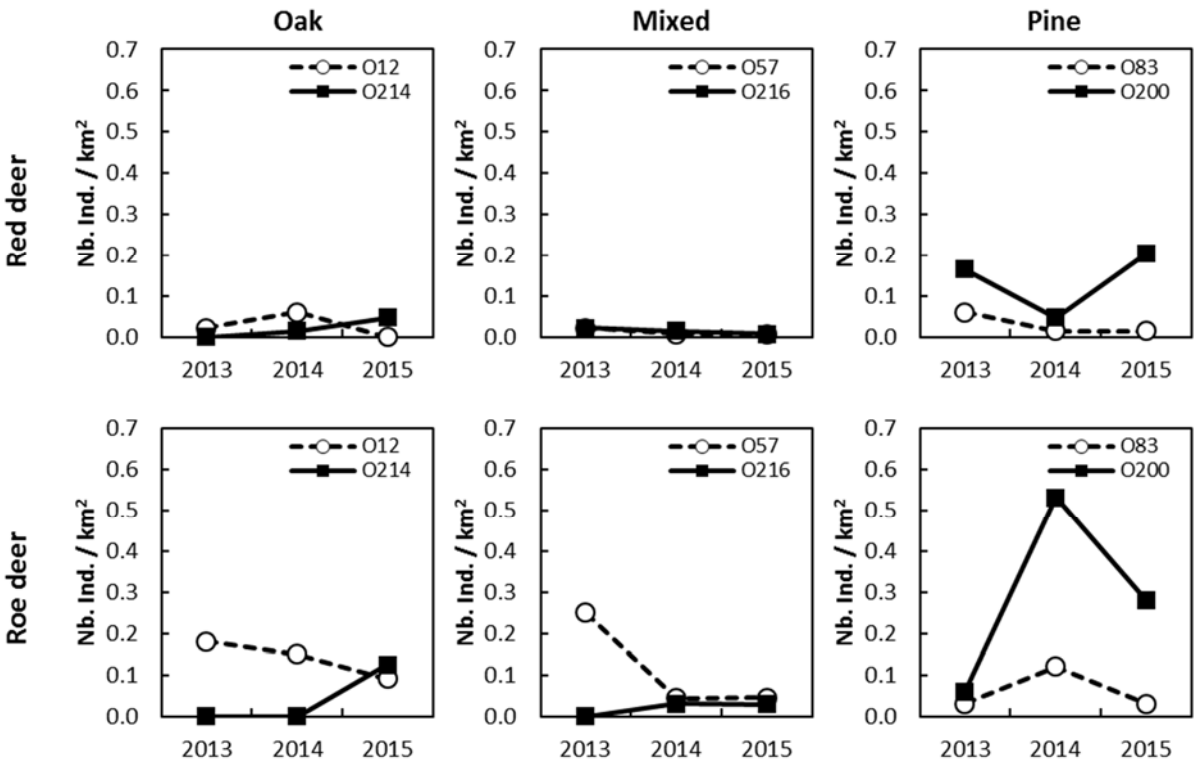
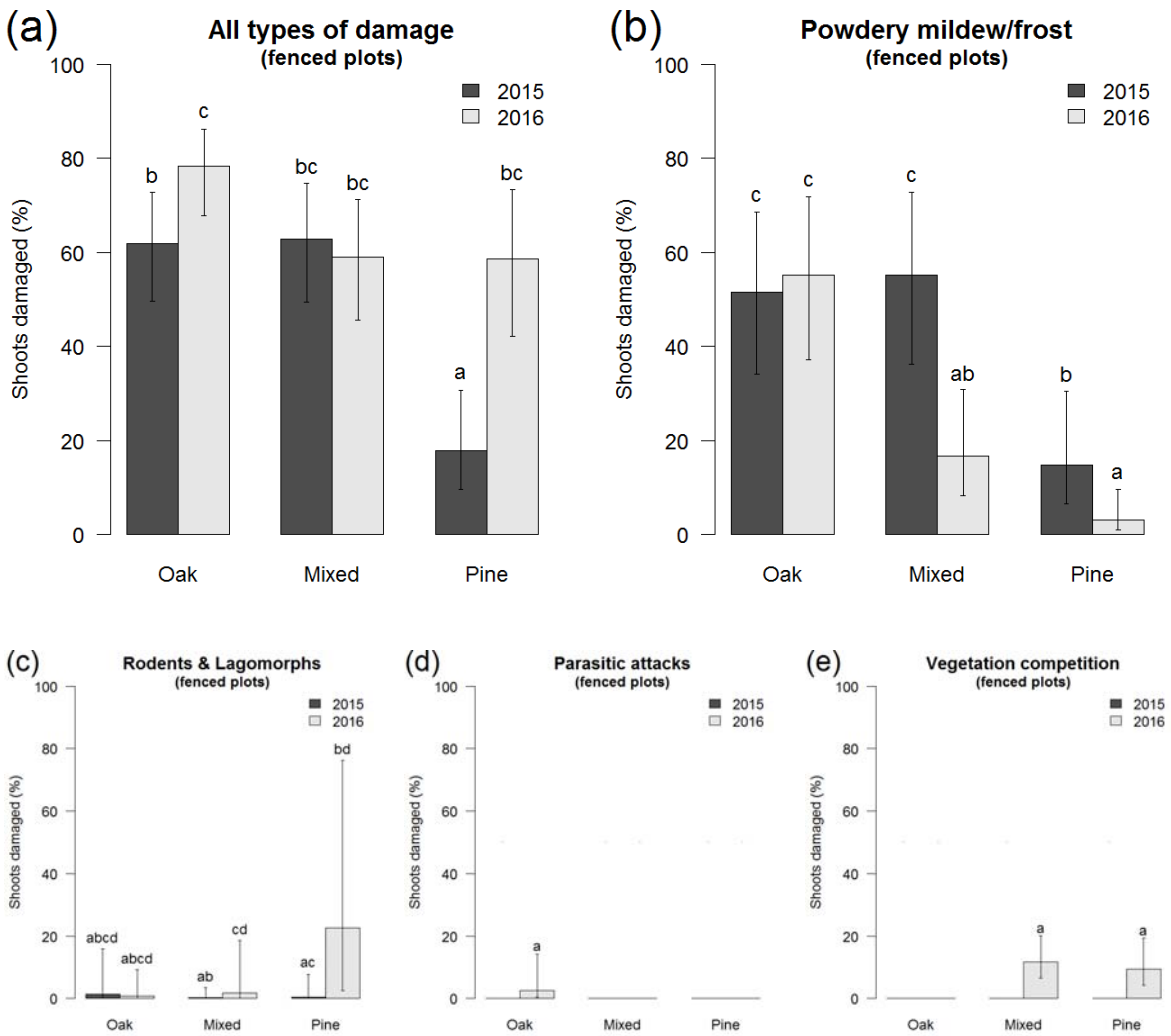
8 Supplementary material

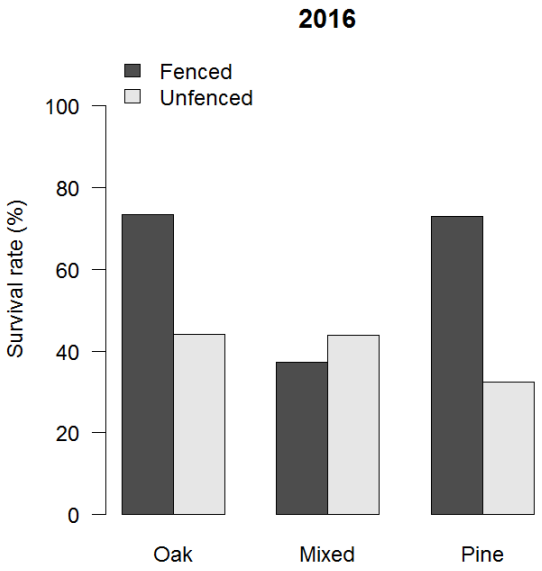


Supplementary Figure 1. Estimated local density of red (*Cervus elaphus* L.) and roe (*Capreolus capreolus* L.) deer at the study plots. A random encounter model (REM) was used to estimate local densities (Rowcliffe et al., 2008; Lucas et al., 2015). Camera trapping was performed during three four-week periods: February-March, May-June and November-December. During each four-week period, a single camera per unfenced study plot was left in place for 6 consecutive days at each corner of the study plot for a total of 24 days of survey per four-week period and 72 days of survey per year. The cameras were placed 2.0 m above the ground. The traps were checked after each 6-day period. The sensor detection zone parameters *r* and θ were estimated at 13.7 m and 45 degrees, respectively. Data on animal speed movement, *v*, was taken from the literature with a mean speed of 1.13 and 0.57 m/s for red and roe deer, respectively (Pellerin et al., 2016). In the 1980s, red deer populations were high and their impact on the forest was judged to be unacceptable by the local forest managers. Since then, the population density has dropped as a consequence of increased hunting efforts and today the local forest managers consider the situation to be satisfactory. This

hunting pressure corresponds to a harvesting level that has maintained a relatively stable deer population for the last ten years.



Supplementary Figure 2. Observed damage other than deer browsing on tagged shoots in fenced plots: (a) all types of damage excluding deer browsing, (b) powdery mildew or frost damage, (c) browsing by rodents or lagomorphs, (d) parasitic attacks such as gall formation and plant tissue losses due to insect herbivory and (e) vegetation competition. All shoots in the unfenced plots were browsed by deer and other types of damages were negligible.



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782 Supplementary Figure 3. Survival rate of oak stumps in late winter 2016 in fenced and unfenced plots

783 based on observed values in monospecific and mixed sessile oak/Scots pine stands.

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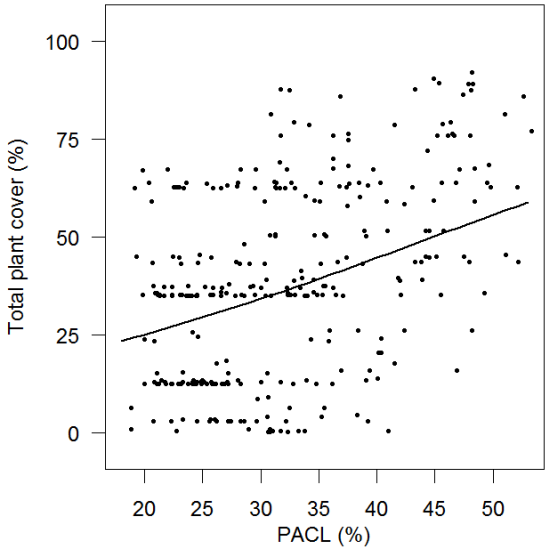

Supplementary Figure 4. Observed correlation pattern between total plant cover and $PACL_{EST}$. Total plant cover is continuous data bounded between 0% and 100%. We therefore used a Beta error distribution (Chen et al., 2006; Chen et al., 2008; Damgaard, 2014) belonging to the glmmadmb function of the glmmADMB package (Fournier et al. 2012, Skaug et al. 2016).

Supplementary Table 1. Summary statistics of models predicting annual growth in length (LENGTH) of the five most vigorous shoots per sessile oak stump in mono-specific and mixed sessile oak/Scots pine stands

Model[§]	N	df	σ_{site}	σ_{plot}	σ_{stump}	$\sigma_{resid.}$	AICc	EF_{full}	EF_{fix}
Null model									
LENGTH = INTERCEPT	563	10	<0.001	381.9	38.4	473.4	4961.8	0.48	
Reference model (experimental design)									
LENGTH = C + H + C × H	**563**	**15**	**<0.001**	**17.9**	**37.0**	**474.2**	**4934.8**	**0.47**	**0.37**
Diameter at breast height of the parent tree (DBH_{parent}) as covariate									
LENGTH = C + H + C × H + DBH_{parent}+ H × DBH_{parent}	**563**	**17**	**<0.001**	**26.4**	**34.7**	**471.3**	**4934.5**	**0.47**	**0.38**
Percentage of above-canopy light ($PACL_{EST}$) as covariate									
LENGTH = C + H + $PACL_{EST}$ + C × $PACL_{EST}$ + H × $PACL_{EST}$	**563**	**17**	**<0.001**	**11.5**	**40.0**	**470.8**	**4932.5**	**0.48**	**0.38**
LENGTH = C + H + $PACL_{EST}$ + C × H + C × $PACL_{EST}$ + H × $PACL_{EST}$	563	19	<0.001	11.4	39.8	471.7	4933.7	0.48	0.38
Total plant cover ($COVER_{TOT}$) as covariate									
LENGTH = C + H + C × H + $COVER_{TOT}$	**563**	**16**	**<0.001**	**13.8**	**37.4**	**476.0**	**4934.7**	**0.47**	**0.37**
LENGTH = C + H + C × H + $COVER_{TOT}$ + C × $COVER_{TOT}$	563	18	<0.001	12.4	35.5	475.3	4934.8	0.46	0.37
LENGTH = C + H + C × H + $COVER_{TOT}$ + H × $COVER_{TOT}$	563	17	<0.001	17.1	37.3	474.5	4935.5	0.47	0.37
LENGTH = C + H + C × H + $COVER_{TOT}$ + H × $COVER_{TOT}$ + C × H × $COVER_{TOT}$	563	21	<0.001	10.5	36.4	476.4	4936.1	0.47	0.38

[§]A first model was fitted to test for differences related to the experimental design (reference model), where stand composition (C), herbivore exclusion (H) and their interaction were fixed terms. The random term was composed of site, study plot nested within site and stump nested within study plot in order to take into account the nested sampling design (paired fenced-unfenced plots). Covariates were added to the model to see whether they improved model fitting or could replace one of the fixed terms in the first model. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc). Only the best models with a difference in AICc of less than 2 are displayed. The most parsimonious models are shown in bold.

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