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SHORT COMMUNICATION

Short-term browsing by roe deer has little effect on survival and growth of sessile oak seedlings

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We studied the effect of roe deer (*Capreolus capreolus*) browsing on the growth and mortality of sessile oak (*Quercus petraea*) seedlings. First, we measured the height and basal diameter, and counted the number of shoots of the 849 seedlings of an experimental plantation, 60 of which were individually protected by fencing. We then introduced two tame roe deer females every day for three weeks from late May to mid-June. Measurements and counts were repeated after roe deer removal, then once again the following winter. We found no significant effect of browsing on mortality, total height, or basal diameter of the seedlings. However, the browsed seedlings exhibited a lower number of shoots despite regrowth observed after roe deer removal. We propose to use the tolerance of oak to deer browsing to promote natural and inexpensive methods, to protect oak during regeneration, such as the spatial arrangement of plants or the use of slash or surrounding vegetation in favourable environments.

Keywords: Roe deer; browsing impact; oak seedlings; experimental study

Introduction

The impact of deer browsing has been highlighted on forest regeneration (Staines & Welch 1984; Ammer 1996; Motta 1996, 2003; Van Hees et al. 1996; Moore et al. 1999; Palmer et al. 2004; Olesen & Madsen 2008), on structure, composition, and vegetation dynamics of the forest understory (Horsley et al. 2003; Joys et al. 2004), on other communities living in the forest (Stewart 2001; Allombert et al. 2005; Gill & Fuller 2007), and more generally on woodland ecology as a whole (Fuller & Gill 2001; Côté et al. 2004).

The impact on seedlings has been shown to depend on site characteristics, including soil richness or preparation (Olesen & Madsen 2008; Bergquist et al. 2009), light intensity regime and composition of the ground vegetation (Gill & Beardall 2001), quantity of surrounding cover (Kay 1993; Moore et al. 1999; Partl et al. 2002), availability and relative quality of alternative food resources (Moser et al. 2006; Miller et al. 2009; Reimoser et al. 2009), and the silvicultural system in place (Reimoser & Gossow 1996).

As shown by Jensen et al. (2012), ungulates may browse seedlings in all seasons, and Kullberg and Bergström (2001) found in a controlled field-based study that the pedunculate oak

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(*Quercus robur*) had the highest degree of winter browsing among eight tree species tested. Nevertheless, Canham et al. (1994) showed that a severe winter clipping on three different tree species had little effect on growth and survival of the seedlings. Similarly, Kullberg and Welander (2003) found that winter browsing had little effect on the growth of pedunculate oak seedlings and caused no mortality during establishment. In contrast, spring browsing may have an effect on seedling growth, as suggested by experimental studies. Braithwaite and Mayhead (1996) showed that survival of sessile oak (*Quercus petraea*) was high despite high intensities of shoot removal over five years, but growth was significantly depressed in the more severe levels of artificial browsing. Chaar et al. (1997) showed that artificial defoliation of the first growth flush reduced the portion of stem produced by sessile oaks during the growing season. Drexhage and Colin (2003) found that browsed sessile oak seedlings had more branches and greater leaf biomass than unbrowsed seedlings.

Unfortunately, most studies have been performed in multi-ungulate systems (Staines & Welch 1984; Ammer 1996; Motta 1996, 2003; Van Hees et al. 1996; Kullberg & Bergström 2001; Joys et al. 2004; Palmer et al. 2004; Focardi & Tinelli 2005; Jensen et al. 2012), making it difficult to distinguish the impacts of the different species on vegetation structure (Bergquist et al. 2009).

Here, we present an experimental study on the impact of roe deer (*Capreolus capreolus*) browsing on survival and growth of sessile oak seedlings. The roe deer is currently the most widespread large wild herbivore in Europe. Since the late 1970s, its populations have increased across Europe, mainly due to changes in land use, a lack of predators, and stricter hunting regulations (Gill 1992a). This increase has ecological and sometimes economic consequences associated with damage in forestry (Gill 1992b; Cederlund et al. 1998; Ward et al. 2004). Part of the damage results from antler rubbing by males, but the main impact is due to browsing of seedlings (Cederlund et al. 1998). Moreover, the sessile oak and pedunculate oak are main tree species of the European forests, occurring from Mediterranean to Scandinavian regions, and constitute the basis of Atlantic oak-woods, a habitat of high importance in the European Union's Habitats Directive (Palmer et al. 2004). We used true instead of simulated browsing because oak seedlings are susceptible to manipulation (Ducousseau, pers. comm.) and clipping cannot simulate real browsing perfectly, deer pulling on shoots with their incisors, or grinding them between their molars, according to their resistance (Bideau & Maublanc 2015).

The aim of the present study was to investigate the response of recently established sessile oak seedlings to roe deer spring browsing. Specifically, we expected (i) browsed seedlings to be unable to entirely replace the lost shoots and (ii) that this would reduce their survival and growth rates albeit slightly.

Methods

Experiment

The study was conducted in an experimental site owned by the INRA (National Institute of Agronomic Research) located at Gardouch (43°22' N 1°40' E) in southwest France.

In winter 2001 we planted 864 containerized sessile oak seedlings from acorns taken in the Bellême forest (northwest France) and sown and reared in the national forestry nursery of Aix-en-Provence (southeast France). The plantation was performed in a 70 m × 70 m enclosure, and consisted of 24 rows of 36 seedlings each (i.e. a row every 2.5 m, seedlings planted 1.5 m from each other). A drip watering system was installed to prevent drying out. The underlying

vegetation, which was regularly mowed, was composed of grasses and forbs, some of which entered the roe deer diet.

At the start of the experiment, that is, from 19 to 23 May 2003 (T_0), we described the 849 surviving seedlings, measuring their height and basal diameter (root collar), and counting their shoots (i.e. the stems of 1 cm length or more, with one or several leaves). No particular attention was paid to the browsing of leader shoots because mortality of the apical bud, changes in the allocation of shoot elongation between several shoots, and changes in dominance occur frequently in oaks (Harmer 1989, 1992; Collet et al. 1997). We then protected 60 seedlings evenly distributed through the plantation, with individual wire fencing.

Afterwards, two tame roe deer females were introduced into the plantation during the daylight hours for three weeks (26 May–15 June 2003), at the end of which they had browsed most of the 789 unprotected seedlings. An experimenter went with them from time to time to make sure they browsed seedlings throughout the plantation. Water was provided ad libitum. In addition, 600 g of artificial roe deer pellets (ca. 90% of the daily needs) was given daily per animal, only in the night pen to encourage the roe deer browsing during the day.

The 60 individual seedling protections were removed at the departure of the roe deer, and from 2 to 6 July 2003 (T_0'), we again measured the height of the seedlings, and counted the number of shoots they carried. Finally, from 5 to 9 January 2004 (T_1), we checked the status (dead or alive) of each seedling, and when alive, performed the same measurements as those made at T_0 .

Statistical analysis

Distributions of height and basal diameter were approximately Gaussian, and their variances did not differ between protected and unprotected seedlings (F -test: P -value between 0.09 and 0.69 depending on the variable and the experimental step). Height and basal diameter were therefore left untransformed irrespective of the analysis. In contrast, shoot number needed to be square-root transformed for its distribution to become more symmetrical, and its variance more homogeneous between samples (F -test: P -value between 0.27 and 0.96 after transformation). Accordingly, shoot number was square-root transformed for all statistical inferences with the exception of correlations.

Height, basal diameter, and (square-root transformed) number of shoots of protected and unprotected seedlings were compared, using the two-sample t -test. Within-sample difference in square-root transformed number of shoots between T_1 and T_0' was tested, using the paired-sample t -test. In order to test whether the between-samples difference in shoot number varied between T_0' and T_1 , we used a linear mixed-effect model with the square-root transformed number of shoots as dependent variable, time (T_0' vs. T_1) and treatment (protected vs. unprotected) as fixed-effect factors, and seedling identity as random-effect factor. Once the model was fitted by maximizing restricted log-likelihood (REML method), we tested for the time*treatment interaction using the F -test.

Pearson's correlations between numbers of shoots at T_1 and T_0' , and T_1 and T_0 were compared, using Williams' t -test (Williams 1959). Fisher's exact test was used for comparing the proportions of protected and unprotected seedlings that survived (/died) between T_0' and T_1 . The effect of shoot number on mortality was analysed, using logistic regression (generalized linear model; dependent variable distribution: binomial; link function: logit) and associated test on deviance.

Table 1. Mean height, basal diameter, and shoot number ($\pm SE$) of the protected and unprotected oak seedlings at times T_0 , T_0' , and T_1 . Between brackets: mean shoot number ($\pm SE$) of the unprotected seedlings alive at T_1 .

	T_0		T_0'		T_1	
	Unprotected	Protected	Unprotected	Protected	Unprotected	Protected
Height (cm)	48.87 $\pm$ 0.29	47.75 $\pm$ 1.10	46.14 $\pm$ 0.31	46.78 $\pm$ 1.21	45.90 $\pm$ 0.36	45.86 $\pm$ 1.32
Collar diameter (cm)	0.91 $\pm$ 0.01	0.88 $\pm$ 0.02	—	—	1.01 $\pm$ 0.01	1.00 $\pm$ 0.03
Shoot number	21.43 $\pm$ 0.32	20.70 $\pm$ 1.12	12.46 $\pm$ 0.27	23.38 $\pm$ 1.36	18.13 $\pm$ 0.35	21.73 $\pm$ 1.37
			(12.70 $\pm$ 0.27)			

All the statistical analyses were performed using R software (R Core Team 2014), and more specifically the nlme package (Pinheiro et al. 2013) for the linear mixed-effect model, and the cocor package (Diedenhofen 2013) for the comparison of correlation coefficients. In the Results section, tests are two-sided unless otherwise specified.

Results

Immediate roe deer impact at T_0'

Before roe deer introduction (T_0), the protected ($n = 60$) and unprotected ($n = 789$) seedlings did not differ in morphology (Table 1; height: $t_{847} = 1.015$, $P = 0.31$; basal diameter: $t_{847} = 1.092$, $P = 0.28$; number of shoots: $t_{847} = 0.638$, $P = 0.52$). After roe deer removal (T_0'), they remained similar in height (Table 1; one-sided t -test: $t_{847} = -0.551$, $P = 0.29$), but unprotected seedlings exhibited a much lower number of shoots than protected seedlings (Table 1; one-sided t -test: $t_{847} = -9.110$, $P < 0.001$).

Figure 1. Mortality rate between T_0' and T_1 as a function of the number of shoots carried by the unprotected seedlings at T_0' . The only protected oak seedling that died carried 29 shoots at T_0' . n : sample size.

Seedling survival at T_1

Survival was high between T_0' and T_1 , and did not significantly differ between protected and unprotected seedlings (protected: 98.3%, $n = 60$; unprotected: 94.3%, $n = 789$; one-sided Fisher's exact test: $P = 0.15$). However, further analysis shows that mortality in unprotected seedlings increased as the number of their shoots at T_0' decreased (deviance: $\chi^2_1 = 16.337$; $P < 0.001$), and became significantly higher than that of protected seedlings when less than 11 shoots remained after browsing (Figure 1; one-sided Fisher's exact test: $P = 0.037$).

Seedling growth at T_1

Protected ($n = 59$) and unprotected seedlings ($n = 744$) that were alive at T_1 exhibited similar heights (Table 1; one-sided t -test: $t_{801} = 0.028$, $P = 0.51$) and basal diameters (one-sided t -test: $t_{801} = 0.314$, $P = 0.62$) but different numbers of shoots (one-sided t -test: $t_{801} = -2.787$, $P = 0.003$). The number of shoots of unprotected seedlings at T_1 showed greater correlation to the number of shoots at T_0' (Figure 2a; $r = 0.637$, $P < 0.001$) than to the number of shoots at T_0 ($r = 0.556$, $P < 0.001$; comparison between the two correlation coefficients: $t_{741} = 2.927$, $P = 0.004$), illustrating a durable effect of browsing on seedling growth. However, the difference in shoot number between protected and unprotected seedlings was lower at T_1 than between the same seedlings at T_0' (Table 1: $F_{1,801} = 47.556$, $P < 0.001$). Indeed, whereas shoot number decreased slightly between T_0' and T_1 in protected seedlings (paired-sample t -test: $t_{58} = -2.631$, $P = 0.011$), it increased on average in the surviving unprotected seedlings (paired-sample t -test: $t_{743} = 19.687$, $P < 0.001$). Increase in shoot number was greater when seedlings had lost a larger number of shoots in the presence of roe deer (Figure 2b; Pearson's correlation: $r = 0.405$, $P < 0.001$).

Figure 2. (a) Shoot number at T_1 as a function of shoot number at T_0' among the unprotected oak seedlings that remained alive. (b) Difference in shoot number between T_1 and T_0' as a function of the difference in shoot number between T_0 and T_0' for the same seedlings.

Discussion

Just before the growing season following the experimental roe deer browsing period, the mortality of unprotected plants was low, and not significantly different from that of protected plants. This result is even more striking when considering the challenging conditions of the severe drought-heat wave of 2003, which led to a lack of growth of all seedlings between T_0 and T_1 despite the drip watering system installed. This high survival rate is in agreement with the results obtained from simulated browsing on pedunculate or sessile oak: the effect of clipping on oak survival remained non-significant after up to five years of treatment (Braithwaite & Mayhead 1996; Harmer 2001). In the same way, little effect of browsing or clipping was found on mortality in European beech (*Fagus sylvatica*, Harmer 2001), Norway spruce (*Picea abies*, Bergquist et al. 2003), and Scots pine (*Pinus sylvestris*, Bergquist et al. 2009). Other tree species may suffer more impact from browsing, as shown by the significant decrease in survival of sycamore maple (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*), or silver birch (*Betula pendula*), after natural or simulated browsing (Harmer 2001; Bergquist et al. 2009).

In the present study, the main impact of deer browsing on oak seedlings was a decrease in the number of shoots. This was significant immediately after the removal of deer and persisted until the following growing season. We did not estimate leaf biomass, but Drexhage and Colin (2003) showed that the leaf contribution to the total biomass was the same for 6–7-year-old browsed (unfenced) and unbrowsed (fenced) sessile oak seedlings, while more biomass was allocated to the stem in unbrowsed plants and to the roots in browsed plants. Van Hees et al. (1996) showed that differences in leaf area between browsed (unfenced) and unbrowsed (fenced) pedunculate oak saplings with the same shoot biomass were not significant, 5–6 years after fencing.

Nevertheless, the regeneration success of oaks in natural conditions may be compromised or at least delayed by a combination of factors including light level, inter-specific competition, and deer browsing (Van Hees et al. 1996; Götmark et al. 2005; Harmer & Morgan 2007; Bergquist et al. 2009). The decrease in the number of shoots may actually lead to delayed growth as reported by most authors in various species (Welch et al. 1992; Van Hees et al. 1996; Harmer 2001; Bergquist et al. 2003, 2009; Vila et al. 2003). Though mortality rate did not differ significantly in our experiment between protected and unprotected seedlings, it became significantly higher in the unprotected plants when less than 11 shoots remained. This trend could become substantial after a few years of browsing. Only long-term studies can establish whether oaks can withstand browsing and competition in forests and recruit into the tall canopies of semi-natural forests. Oaks are known to survive repeated partial removal of the above-stump parts by resprouting (Braithwaite & Mayhead 1996; Harmer 2001) and Götmark and Kiffer (2014) showed that oaks can regenerate in the long term among competing tree species (especially shade-tolerant trees) and under browsing pressure from herbivores.

This tolerance of oak to browsing in favourable environments should allow the use of natural methods of protection, such as the spatial arrangement of preferred plants in relation to less preferred ones (Moore et al. 1999; Bergman et al. 2005) or the use of slash or surrounding vegetation as physical protection or attractive alternative food (Hay 1986; Buckley et al. 1998; Milleret et al. 2006; de Chantal & Granström 2007; Gómez-Aparicio et al. 2004; Götmark et al. 2011; Jensen et al. 2012). As suggested by Ward et al. (2008), these efforts to protect oak regeneration should be combined with deer population management based on reliable index-based methods (Morellet et al. 2007), allowing deer densities to be matched with habitat capacities.

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