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Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks

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Abstract

Acorn sowing is a reforestation technique that can potentially render high-quality oak seedlings and high seedling survival, although it is often discarded due to high rates of seed predation. Predator activity can be modified by habitat complexity due to its effect on accessibility and protection for different predators. In this study we analysed how habitat complexity generated by different post-fire management treatments, sowing depth, and capsaicin (a chemical repellent) affect acorn predation by two guilds of post-dispersal predators that differ in size and foraging behaviour. We carried out two acorn predation experiments. In Experiment #1 we buried acorns at two depths (2 and 8 cm) in two post-fire burnt-wood management treatments of different habitat complexity, namely: 1) Salvage Logging (SL), where the burnt trunks were cut and piled and the branches were masticated (lower habitat complexity), and 2) Non-Intervention (NI), with no action after the fire and 100% of the trees naturally fallen by 2009, thus leaving a habitat with lying burnt logs and branches (higher habitat complexity). In Experiment #2 we repeated Experiment #1, with the addition of capsaicin as a mammal repellent treatment. Most acorns were consumed in both years (ca. 90%), mainly by rodents. In Experiment #1 predation by boars accounted for 4.1% of overall predation, and it was about twice as high in SL than in NI, likely due to the physical difficulty for large mammals to forage in an area with a complex structure created by lying logs and branches. In contrast, rodents consumed ca. 1.4 times more acorns in NI than in SL, which led to overall greater predation in NI in both experiments. This was likely due to the protection provided by the branches for the rodent community. Deeper burial reduced predation by small percentages, although in Experiment #1 it had a negligible effect in NI. Capsaicin did not reduce predation, and it reduced seedling emergence to half. This study suggests that habitat complexity created by trunks and branches reduced predation by wild boars, but favoured rodent acorn predation. We conclude that other methods for the protection of individual acorns need to be identified to increase the success of oak reforestation via seeding.

Keywords: acorn removal, capsaicin, post-fire management, rodents, seed predation, seed sowing

Abbreviations: BWM= Burnt-wood management treatment(s); SL= Salvage Logging treatment; NI= Non-Intervention treatment

1. Introduction

Seed sowing and seedling planting are universal methods for the restoration of woody plant species in disturbed areas (Twedt and Wilson, 2002; Pausas et al., 2004; Dey et al., 2008; Cortina et al., 2009). Planting has the advantage of using already emerged seedlings. It avoids mortality from seed predation, which otherwise acts as a filter that can destroy a great proportion of available seeds (Crawley and Long, 1995; Herrera, 1995; Gómez, 2004; Pulido and Díaz, 2005), and consequently hinder regeneration via seeding. However, planting has the major inconvenience of being far more costly and time-consuming than seeding (Bullard et al., 1992; Stanturf et al., 2000; Espelta et al., 2003; Allen et al., 2004). Through seeding, many seeds can be sown in little time and at a relatively low cost, and in case they escape seed predation, high germination rates and adequate seedling performance can be obtained (Fuchs et al., 2000; Pulido and Díaz, 2005; Cortina et al., 2009; Puerta-Piñero, 2010). Even if part of the sown seeds are lost before reaching the seedling stage (e.g. by predation or fungal attack), the higher number of seeds that can be sown, compared to the seedlings that can be planted at a similar cost, might compensate (Bullard et al., 1992; Pausas et al., 2004).

Oak woodlands are one of the main vegetation types in the Northern Hemisphere. These forests have suffered disturbances during millennia, and currently they are one of the main targets in restoration policy (e.g. EEC Regulation No. 2080/92; US Wildlife Habitat Incentives Programs). The most common oak reforestation technique is via plantations of nursery-grown seedlings (King and Keeland, 1999; Espelta et al., 2003; Cortina et al., 2009; Del Campo et al., 2010). However, survival of planted seedlings may be low, particularly in the case of ecosystems with a dry summer such as those under Mediterranean climate conditions (Rey Benayas et al., 2005; Castro et al., 2006; Valdecantos et al., 2006; Del Campo et al., 2010). Besides, nursery-grown oak seedlings often suffer suboptimal root architectures which are not appropriate for Mediterranean drought conditions (Peman et al., 2006; Dey et al., 2008; Tsakaldimi et al., 2009). Furthermore, planting, associated with machinery removing naturally established vegetation and digging holes on mountain slopes, usually causes important damage to the soil (Pulido, 2002; Espelta et al., 2003). In some cases, machines are not even capable of entering certain areas due to the steep slopes, while a person would not have difficulties in passing and sowing acorns. These arguments question whether the investment in oak planting and subsequent management is actually worthwile compared to seeding.

Acorn sowing is largely discarded for oak reforestation due to the high seed loss produced by vertebrate predators (Allen et al., 2004; Pulido and Díaz, 2005; Dey et al., 2008; Cortina et al., 2009), including small rodents (Gómez, 2003; Tyler et al., 2006; Puerta-Piñero et al., 2010a), wild ungulates (such as wild boars, *Sus scrofa* and red deer, *Cervus elaphus*), and livestock (Schmidt and Timm, 2000; Muñoz and Bonal, 2007; Gómez and Hódar, 2008; Puerta-Piñero, 2010). However, the emergence rate of surviving acorns after sowing tends to be high (Fuchs et al., 2000; Allen et al., 2004; Pulido and Díaz, 2005). In addition, the survival rates of emerged oak seedlings can be similarly high, with values that can surpass 50% and even approach 100% several years after sowing (Tietje et al., 1991; Pulido and Díaz, 2005; Mendoza et al., 2009; Matías et al., 2011). Seedlings emerged from acorns in the field tend to develop better root architectures for field conditions (Allen et al., 2004; Dey et al., 2008; Tsakaldimi et al., 2009). Another advantage of sowing is that it provides flexibility, as the temporal span when acorns can effectively be sown is wider than that of planting (Allen et al., 2004). Seeding may also result in less vegetation uniformity of the reforested area, potentially resulting in better wildlife habitat (Twedt and Wilson, 2002). Thus, seed sowing has the potential to be an effective and cost-efficient method for oak woodland restoration if seed predation was reduced. Consequently, finding a way for acorns to overcome post-dispersal seed predation is a key issue that could promote oak woodland reforestation (Schmidt and Timm, 2000; Gómez, 2004; Smit et al., 2008).

The management of habitat complexity is a way to influence plant-animal interactions, including the potential reduction of post-dispersal seed predation on sown seeds. Movement decisions and foraging behaviour of animal species are affected by habitat complexity (Fuchs et al., 2000; Gómez, 2004; Puerta-Piñero, 2010; Puerta-Piñero et al., 2010a). Indeed, the same habitat characteristics may affect different guilds of predators in different ways (Matías et al., 2009; Smit et al., 2008; Puerta-Piñero, 2010). For instance, small seed predators such as rodents tend to concentrate their activity in areas with a rather complex habitat structure, as this reduces the risk of predation they perceive (Schupp, 1988; Torre and Díaz, 2004) and provides more suitable conditions for them (Haim and Izhaki, 1994). By contrast, seed predation by large mammals such as ungulates could be lower where a higher habitat complexity impedes their movements and partially avoids their penetration (Forget et al., 2005; Gómez and Hódar, 2008; Smit et al., 2008; Puerta-Piñero, 2010).

Besides managing habitat complexity at larger landscape scales, acorn-scale solutions such as deep sowing or the use of chemical repellents could also improve seed survival. Burial can increase the likelihood of surviving to acorn predation (Crawley and Long, 1995; Herrera, 1995; Fuchs et al., 2000; Gómez, 2004; Pulido and Díaz, 2005). Buried acorns can also find more favourable temperatures and moisture levels than on the ground surface (Li and Ma, 2003; Tietje et al., 1991; Dey et al., 2008), and this positive effect is likely to increase up to a certain depth (Tietje et al., 1991; Fuchs et al., 2000). The use of chemical substances that act as predator repellents is another technique to reduce predation that has been little explored (Nolte and Barnett, 2000; Willoughby et al., 2011). Capsaicin is a natural repellent obtained from chilli peppers (genus *Capsicum*; EPA, 1996) that produces a burning sensation in mammals by irritating mucose tissues, and it has successfully been used as a mammal repellent under controlled conditions (e.g. Nolte and Barnett, 2000; Willoughby et al., 2011). However, the capacity of this substance to reduce seed predation has scarcely been tested under field conditions (but see Barnett, 1998).

In this study we investigate whether the effectiveness of seed sowing could be enhanced in landscapes managed to reduce predation by large mammals while individual acorns are protected to minimise their predation by rodents. For this, a post-fire landscape was managed to create two treatments differing in habitat complexity: one where all the burnt trees were removed (the usual post-fire treatment, called salvage logging, with low habitat complexity), and one where burnt wood was left *in situ* creating a complex mesh of fallen logs and branches (high habitat complexity). We hypothesised that i) acorn predation would vary among burnt-wood management treatments, ii) deeper-buried acorns would suffer lower predation rates, and iii) capsaicin would deter predation on acorns. As a result, we aimed to explore whether appropriate management of burnt wood, sowing depth, and the use of chemical repellents could create a suitable scenario for the restoration of oak forests through seed sowing.

2. Materials and methods

2.1. Study site and species

The study site is located in the Sierra Nevada National Park, SE Spain, where a fire burned 1300 ha of pine forest (3420 ha in total) in September 2005. The site was located in an affected *Pinus pinaster* and *P. nigra* reforestation stand at 1477 m a.s.l. (36º 57' 9.8949 N, 3º 29' 36.2381'' W) located in the Lanjarón municipality. Pine tree density in the study area was 1477 ± 46 individuals ha^{-1}, with a basal trunk diameter of 17.7 ± 0.2 cm (mean ± SE; Castro et al., 2011). It is situated on a SW-oriented hillside (slope: 30.3 ± 5.7%) with micaschist as bedrock. Climate in the area is Mediterranean, with warm, dry summers and mild, rainy winters. Mean annual precipitation recorded at the site was 501 ± 49 mm (1988-2011) and mean annual temperature was 12.3 ± 0.4 °C (1988-2008). The study years (2010 and 2012) greatly differed in terms of precipitation. Precipitation from January through June 2010 (time period of the experiments) was 555.7 mm, while in 2012 it was only 145.1 mm during the same months.

Holm oaks (*Quercus ilex* subsp. *ballota* L.) naturally coexisted with the pines in the study area, and are considered the potential climax vegetation of the area according to climatic, edaphic and historical data (Valle, 2003). The holm oak is a sclerophyllous evergreen tree, abundant in the Mediterranean area of the Iberian Peninsula. Acorns ripen in autumn and are dispersed primarily by the European jay *Garrulus glandarius* (Castro et al., 2012). The main post-dispersal acorn predators in the area are wild boars and rodents such as *Apodemus sylvaticus* and *Mus spretus* (Gómez and Hódar, 2008; Puerta-Piñero et al., 2010a; Unpublished data).

2.2. Experimental design

Seven months after the fire (April 2006), the local Forest Service established a plot with three randomly distributed replicates of two treatments that differed in their degree of post-fire burnt-wood management (BWM hereafter) and thus in the resulting post-fire habitat complexity (Fig. 1):

1) Salvage logging (SL). In this treatment, all the burnt trees were cut and their trunks cleared of their main branches using chainsaws. Trunks were piled in groups of 10-15 and left *in situ*, and the woody remains were treated with a mechanical masticator. This created an open landscape where ungulates could move and forage easily (Puerta-Piñero et al., 2010a).

2) Non-Intervention (NI). Here the burnt trees were left standing and no further action was taken. Trees fell naturally, with a cumulative fall rate (measured with 100 marked pines per replicate in February of each year) of 0.0% in 2006, 12.33 ± 3.38% in 2007, 92.88 ± 1.18% in 2008, and 100% in 2009 (Castro et al., 2012). Thus, during the study period (2010 and 2012), this treatment was characterised by a complex structure of trunks and branches spread all over the ground.

The six replicates had an average size of 2.0 ± 0.2 hectares, with no significant differences in size between treatments (Kruskal-Wallis test).

2.3. Habitat complexity

In 2012, we sampled habitat complexity in the experimental BWM treatments. For this we established eight linear transects of 25 m in each of the thee replicates of both treatments. The transects were defined by randomly selecting eight starting points within each replicate, and drawing a straight line in the direction of the maximum slope. We noted the nature of the highest contact (soil, live plants, or woody debris) and its height every 0.5 m along each transect as well as at 1 m to both sides of the transect (thus 150 points per transect). Height was categorised in six different classes (0= 0 cm; 1= 1-10 cm; 2=11-25 cm; 3= 26-50 cm; 4= 51-100 cm; 5= >100 cm).

2.4. Acorn Predation Experiments

We studied acorn predation in two complementary experiments performed in 2010 (Experiment #1) and 2012 (Experiment #2).

Experiment #1 was carried out to investigate the combined effects of post-fire BWM and depth of burial on acorn predation. It was set up in January 2010. We sowed 150 viable acorns per replicate of each treatment (900 acorns monitored in total). Half of the acorns in each replicate were sown at 2 cm depth (shallow, hereafter), mimicking biotic dispersal (Gómez, 2003; Muñoz and Bonal, 2007), and the other half at 8 cm (deep, hereafter), which simulates potential human sowing for reforestation purposes (Allen et al., 2004; Dey et al., 2008). Acorns were individually placed within the replicates, at least 10 m apart from each other, and at alternated sowing depths. Burial holes were made with a pick, removing the ground as little as possible. A numbered wooden stick was set into the ground to mark the buried acorn. Viability of the acorns was checked before sowing through the flotation method (Gómez, 2004). We monitored acorn removal after 10, 40, and 90 (± 3) days of sowing. In each revision, the fate of the acorns was visually recorded (predated vs. non-predated), as well as predator identity (rodent vs. wild boar). The latter is easily identifiable, as rodents dig a narrow hole to unbury the acorns, while wild boars leave plants uprooted and the soil turned over (Puerta-Piñero, 2010). In the last revision, performed at the time of germination, we confirmed the removal of acorns by digging 40 randomly selected sowing points per BWM replicate with a pick. In 100% of the cases we confirmed that the results of the visual revision had been correct. Removed acorns were considered predated because previous studies found that > 98% of acorns found by rodents are finally predated and that there is no secondary caching by the main acorn dispersers in the area (Muñoz and

Bonal, 2007; Gómez et al., 2008). Out of the 900 experimental acorns, 14 were lost during the study, so the statistical analyses were made on the remaining (N = 886).

Experiment #2 was carried out to test the effects of burial depth in both BWM treatments (as in Experiment #1), combined with the use or not of capsaicin as a rodent repellent. It was performed in January 2012. We used the same post-fire BWM replicates and burial depths as in Experiment #1. Natural capsaicin (65% capsaicin, 35% dihydrocapsaicin) was obtained from Sigma-Aldrich. We diluted it in an emulsion of diethyl ether and sorbitan trioleate at 24 g l^{-1} (Willoughby et al., 2011). We applied a total of 0.325 g of capsaicin per kg of acorns, a proportion that has been shown to be effective in controlled multiple-choice experiments with mice and squirrels on wheat (Willoughby et al., 2011). For each experimental combination (BWM x burial depth x capsaicin) we sowed 35 acorns, totalling 840. Acorns within each BWM replicate were placed at systematically alternated depth x capsaicin combinations. Methods were as described above. One visual revision was made 7 +/- 2 days after sowing. A second visual revision was made by the time of germination in May, 100 +/- 7 days after sowing. After this last revision we again confirmed acorn removal by digging up 40 randomly selected sowing points per BWM replicate with a pick, and again we confirmed 100% of accuracy of the visual revision. Five acorns were lost during the study, so our effective sample size was N = 835.

2.5. Effect of capsaicin on seedling emergence

At the time of sowing in the field in Predation Experiment #2, we performed an experiment to test the effect of capsaicin on seedling emergence. A total of 80 acorns (40 treated with capsaicin as described above and 40 control with no capsaicin added) were sown in plastic containers using a substrate prepared by mixing 67% natural soil from the experimental plot in Lanjarón and 33% sand. Acorns were planted at 6 cm depth, using an alternating distribution. The experiment was conducted in a nursery at outdoor conditions near the University of Granada (735 m a.s.l.). The containers (300 cm^3) were covered with wire mesh to prevent predation by domestic rodents, and were periodically irrigated during the trial. We monitored their emergence after 60, 80, 86, 94, 103, 114, and 154 days.

2.6. Data analyses

Habitat structure was analysed with hierarchical ANOVAs that used percentage cover of each cover type (soil, live plants, wood) as dependent variables, with all height classes pooled. BWM was the only explanatory factor, and we specified the sampling error structure [sides of a transect (left, centre, right) within transects within BWM replicates]. The percent cover data were arcsine-transformed prior to analysis.

Acorn predation at the end of Experiment #1 was analysed using a generalized linear model (GLM) with binomial response and logit as link function, considering the effects of BWM, Depth, the BWM by Depth interaction, and Replicate nested in BWM. The effect of predator identity was later tested with contingency analysis. For Experiment #2 a similar model was built, using BWM, Depth, Capsaicin, all the possible interactions among these factors, and Replicate nested in BWM as explanatory factors. These models were simplified following Crawley (2007).

We performed a survival analysis to test the effect of capsaicin on seedling emergence with time after sowing. For this we used a GLM with gamma errors. We used Capsaicin as the only explanatory factor. For the final values of acorn emergence, we fitted a GLM with quasi-binomial errors and Capsaicin as explanatory factor.

Statistical analyses were performed using R version 2.15.0 (R Development Core Team, 2012).

3. Results

3.1. Habitat complexity

Open soil covered 39.2 ± 6.0% in SL (mean ± SE of the mean, calculated using the means of the three replicates) and 25.6 ± 4.8% in NI (Table 1), although this difference was not significant ($P > 0.05$). Cover of live plants did not significantly vary with BWM either ($P > 0.05$), and had values of 46.8 ± 7.2% in NI and 49.7 ± 7.2% in SL (Table 1). In contrast, cover of woody debris was significantly greater in NI (27.6 ± 2.8%) than in SL (11.1 ± 2.4%; $F = 18.55$; df = 1; $P = 0.02$).

3.2. Acorn predation experiments

Acorn predation for Experiment #1 reached an overall value of 41.3 ± 1.7% after 10 days, 78.8 ± 1.4% after 40 days, and 87.6 ± 1.1% after 90 days (mean ± SE of the mean). Predation by the end of the experiment was significantly affected by all factors (Table 2). Predation was higher in NI (99.1 ± 0.4%) than in SL (76.1 ± 2.0%), and was slightly greater at 2 cm (89.7 ± 1.4%) than at 8 cm (85.5 ± 1.7%) depth. There was a significant BWM x Depth interaction, as depth had a stronger effect in SL than in NI (Table 2; Fig. 2). Predation was greater in some replicates of the BWM treatments than others, this effect being highly significant (Table 2; Fig. 3). Rodents accounted for 95.9% of the predated acorns, while wild boars consumed the remaining 4.1% (differences among predator agents: $\chi^2 = 652.28$, d.f. = 1, $P < 0.0001$). Predation by rodents was similarly affected by all factors (Table 2), with higher values in NI than in SL (96.8 ± 0.8% vs 70.9 ± 2.2%, respectively). In contrast, predation by wild boars in

NI was about half what it was in SL (2.3 ± 0.7% and 5.0 ± 1.0%, respectively; χ^2 = 4.78, d.f. = 1; P = 0.03).

In Experiment #2, 80.1 ± 1.4% of the acorns had been consumed after 7 days, and 90.0 ± 1.0% at the end of the experiment. Only BWM, Depth and Replicate had a significant effect on predation (Table 3). Predation was greater in NI (99.8 ± 0.2%) than in SL (80.2 ± 2.0%), and slightly greater for shallow (91.6 ± 1.4%) than for deep acorns (88.5 ± 1.6%). Capsaicin did not have a significant effect (Table 3), not even in the first revision (χ^2 = 1.7, P = 0.19; rest of the model not shown). Overall, only 3 acorns were consumed by wild boars (all in SL), and the remaining by rodents.

3.3. Effect of capsaicin on seedling emergence

Capsaicin significantly delayed average emergence time by 9 days (df = 1, χ^2 = 0.52, P = 0.001; Fig. 4). Besides, capsaicin application reduced the final values of seedling emergence from 63% to 33% (df = 1; F = 7.1; P = 0.009).

4. Discussion

We analysed the effect of the habitat complexity generated by different burnt-wood management treatments on mammal acorn consumption in a burnt Mediterranean forest, as well as the potential of sowing depth and the use of capsaicin for reducing acorn predation. We had initially hypothesised that an appropriate habitat management, combined with deeper sowing and/ or the use of a chemical repellent could provide a window of opportunity for oak reforestation via sowing. However, contrary to our expectation, predation rates were very high in all experimental combinations, reaching an overall value of ca. 90% in both years. Nevertheless, our results still provide useful insights to be considered for oak reforestation via acorn sowing.

4.1. Effect of burnt-wood management and sowing depth

Our results show that acorn predation was greater in the treatment with higher habitat complexity generated by logs and branches spread on the ground (NI). On the other hand, predation was reduced with deeper burial, although this difference was generally low and in Experiment #1 it was more apparent in the treatment with lower structural complexity (SL) and negligible in NI. All this may be explained by the foraging behaviour of the main predator guild. On one hand, rodents accounted for most of the predation (nearly 100% in Experiment #2) and they predated very fast, with values that could surpass 70% after just one week. This reduced the opportunities for predation by larger and less abundant mammals such as ungulates. Greater predation rates in NI could be related to potential benefits obtained by the rodent community, as the woody debris on the ground created a habitat where rodent populations could profit from more abundant food, shelter, and nest sites, as well as better thermoregulatory conditions (Herrera, 1995; Loeb, 1999; Smit et al., 2008). Furthermore, the logs and branches could have led to a lower perceived predation risk (Torre and Díaz, 2004; Muñoz and Bonal, 2007). Non-intervention areas could consequently both sustain greater rodent abundances, as well as change rodent foraging behaviour by allowing them to spend more time foraging and digging than in salvage logged areas (Haim and Izhaki, 1994; Torre et al., 2002; Muñoz and Bonal, 2007). A more careful search for food would consequently explain the lower effectiveness of deeper burial obtained in NI in Experiment #1.

Predation by wild boars was low in this study. However, the results support that the management of burnt wood could help reduce acorn losses to this predator, as in Experiment #1 the NI treatment reduced predation by wild boars to half. This was likely due to the physical difficulty for a large mammal to forage in an area with a complex structure created by logs and branches (Relva et al., 2009; Puerta-Piñero, 2010; Puerta-Piñero et al., 2010a). As wild boars can represent a major threat for oak reforestation via seed sowing (Gómez, 2004; Pulido and Díaz, 2005; Smit et al., 2008), the higher post-fire habitat complexity could represent a relevant benefit for reforestation under circumstances of greater predation pressure by these ungulates.

In short, both experimentally tested burnt-wood management practices generated trade-offs between acorn predation by the two different predator guilds. A high habitat complexity created by elements that hamper ungulate foraging may greatly reduce the potential impact of this guild. In contrast, rodents can benefit from the protection of logs and branches, causing high predation even on deeper-sown acorns. The actual effect of burnt-wood management on seeding outcomes will thus depend on the spatial and temporal context of predator abundances.

4.2. Effects of capsaicin on acorn predation and seedling emergence

The application of capsaicin did not reduce acorn predation. This contrasts with previous studies that have shown its effectiveness as a mammal repellent in other situations (Nolte and Barnett, 2000; Jensen et al., 2003; Willoughby et al., 2011). The absence of an effect of capsaicin was evident even one week aftert sowing, so we may discard a potential loss of effectiveness with time due to field conditions. The lack of an effect of capsaicin despite using the same application methods as Willoughby et al. (2011) in multiple-choice feeding trials could be explained by two main hypotheses. First, under field conditions rodents might not have a sufficient natural food supply as to reject the repellent-treated alternative. In the cited cafeteria experiment rodents had a plentiful supply of untreated food, and this could have led them to be more selective than in our study. Second, this effect could have been exacerbated by a potential food shortage in 2012, the year in which capsaicin was applied. Precipitation from January through June 2012 measured at the experimental site was about one-fourth of the precipitation in those months in 2010. The drought during the 2012 rainy season could have led to an even lower food supply for the rodent community, which in turn would have become less selective and searched more carefully for any available food (Puerta-Piñero et al., 2010b). This idea is supported by the results of the first revision of our experiments, as predation by rodents occurred much faster in 2012 than in 2010. Besides not reducing acorn predation, capsaicin reduced seedling emergence by half. This result is in accordance with some studies which have found that the application of capsaicin reduced seed germination of other species (Barnett, 1998; Siddiqui and Uz-Zaman, 2005) but disagrees with others (Gosling and Baker, 2004). However, we are not aware of previous studies addressing the effects of capsaicin on the germination or emergence rates of *Quercus* seeds. According to our results, capsaicin does not seem to be an effective way for promoting oak reforestation.

4.3. Conclusions and insights for future research

Our results show that burnt-wood management and burial depth interact in complex ways and that their potential benefits for oak reforestation via seed sowing depend on the abundance of the different predator guilds. Although the impact of wild boars on sown acorns was low in our site, the opposite could be the case in other situations. Alternatives to control the activity of wild boars (and potentially of other ungulates) such as fencing (Dey et al., 2008) are expensive and in many cases logistically very difficult if possible to carry out. In contrast, burnt logs and branches are common elements after a fire. They come at no additional economic cost, and their use as physical structures to protect acorns against ungulate predation could be useful for oak reforestation. On the other hand, the presence of the burnt wood in our study favoured predation by rodents, and even eliminated the potential benefit of deeper burial. As rodents were by far the most important predator guild, burnt-wood management can be a way to increase seeding success only if effective methods to protect individual acorns from rodents are implemented. Capsaicin was not an appropriate method, as it did not protect against acorn predation and it even reduced seedling emergence.

We suggest that more research should be conducted in two lines. First, other methods to protect individual acorns should continue to be explored for both their ecological and their economic efficacy. These methods could include small fences (Crawley and Long, 1995; Tietje et al., 1991), wire mesh screens (Schmidt and Timm, 2000; Dey et al., 2008), or other repellents (Nolte and Barnett, 2000; Willoughby et al., 2011). Second, we need to better understand the population trends of predators with post-fire succession. For example, the rodent community may disappear after a fire (Fons et al., 1993; Haim and Izhaki, 1994), and the succession of recolonisers may differ under distinct burnt-wood management (Haim and Izhaki, 1994). This temporal gap could be regarded as a window of opportunity for acorn sowing coupled with the greater habitat complexity achieved by burnt-wood management to deter ungulate predation.

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Figure legends

Figure 1. Photographs of the burnt-wood management treatments: a) Salvage Logging, and b) Non-Intervention. The fire occurred in September 2005, treatments were implemented in spring 2006, and the photos are from 2012. Photo a) courtesy of R. Marzano, photo b) by JC.

Figure 2. Percent acorn predation in the Non-Intervention (NI) and the Salvage Logging (SL) post-fire management treatments in 2010. Graphs show differences between deep (8 cm) and shallow (2 cm) buried acorns for both treatments. The dark grey areas on the upper part of the bars indicate predation by boars, and the lower part by rodents. Note that mean differences between deep and shallow acorns were larger in the SL than in the NI treatment.

Figure 3. Spatial distribution of predated (grey points) and non-predated (black points) acorns sown at (a) 2 cm and (b) 8 cm depth in 2010. Post-fire treatments are Salvage Logging (SL) and Non-Intervention (NI).

Figure 4. Percent seedling emergence with and without the application of capsaicin. These acorns were sown in plastic containers and isolated from predators, and emergence was monitored.

Table 1. Indicators of habitat complexity in the Salvage Logging and Non-Intervention burnt-wood management treatments. Numbers in the table indicate the percentage of sampling points that had their highest contact at the specified combination of height and structural element. Note that only the highest contact at each sampling point was recorded. An increase in woody cover at greater height classes in NI relative to SL can be observed.

Non-Intervention					Salvage logging				
	Structural element					Structural element			
Height (cm)	Open soil	Live plants	Wood	Total	Height (cm)	Open soil	Live plants	Wood	Total
0	25.6	0.0	0.0	25.6	0	39.2	0.0	0.0	39.2
1-10	0.0	3.6	2.1	5.8	1-10	0.0	6.4	5.2	11.6
11-25	0.0	5.2	6.2	11.4	11-25	0.0	6.2	2.8	9.0
26-50	0.0	11.2	9.9	21.1	26-50	0.0	11.3	1.9	13.2
51-100	0.0	20.0	7.1	27.1	51-100	0.0	22.3	1.1	23.4
>100	0.0	6.8	2.2	9.0	>100	0.0	3.5	0.0	3.5
Total	25.6	46.8	27.6	100.0	Total	39.2	49.7	11.1	100.0

Table 2. Generalized Linear Model with the effects of burnt-wood management treatment (BWM: Non-Intervention and Salvage Logging), acorn sowing depth (shallow: 2 cm vs. deep: 8 cm), and replicate nested in BWM on overall acorn predation (all predators) and predation by rodents alone in Experiment #1 (2010).

		Overall predation		Predation by rodents	
	d.f.	χ^2	P	χ^2	P
Treatment (T)	1	131.57	**<0.0001**	124.46	**<0.0001**
Depth (D)	1	4.00	**0.05**	5.23	**0.02**
T x D	1	4.20	**0.04**	5.00	**0.03**
Replicate [T]	4	82.40	**<0.0001**	72.56	**<0.0001**

Table 3. Generalized Linear Model with the effects of burnt-wood management treatment (BWM: Non-Intervention and Salvage Logging), acorn sowing depth (shallow: 2 cm vs. deep: 8 cm), application of capsaicin, and BWM replicate nested in treatment on overall acorn predation in Experiment #2 (2012).

Term	df	χ^2	P
Treatment (T)	1	114.1	**<0.0001**
Depth (D)	1	4.7	**0.03**
Capsaicin (C)	1	1.8	0.18
D x C	1	0.1	0.82
D x T	1	0.8	0.36
C x T	1	1.0	0.31
T x D x C	1	0.0	1
Replicate [T]	4	182.7	**<0.0001**

Figure 1

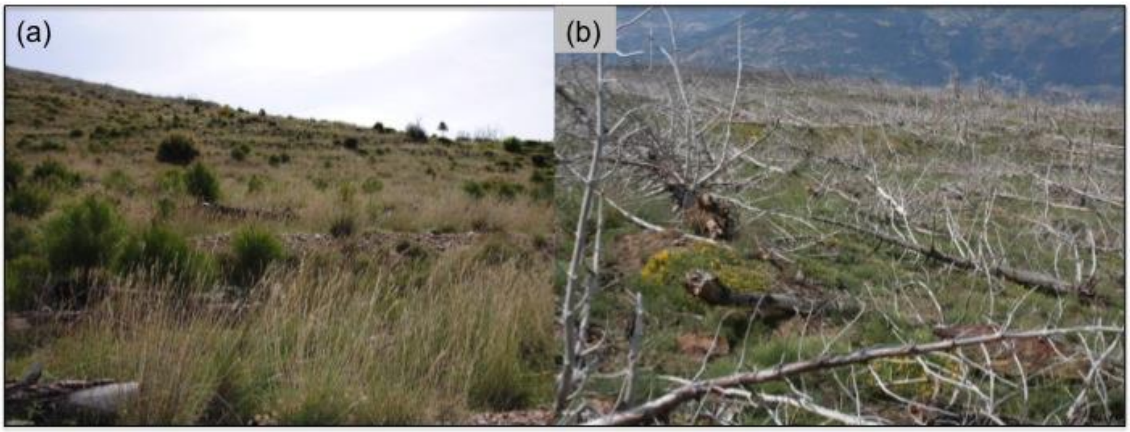


Figure 2

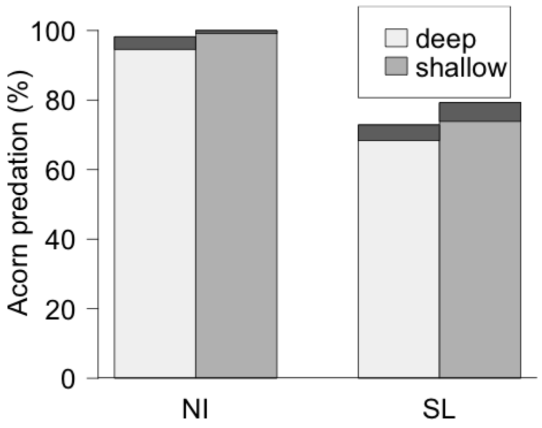


Figure 3

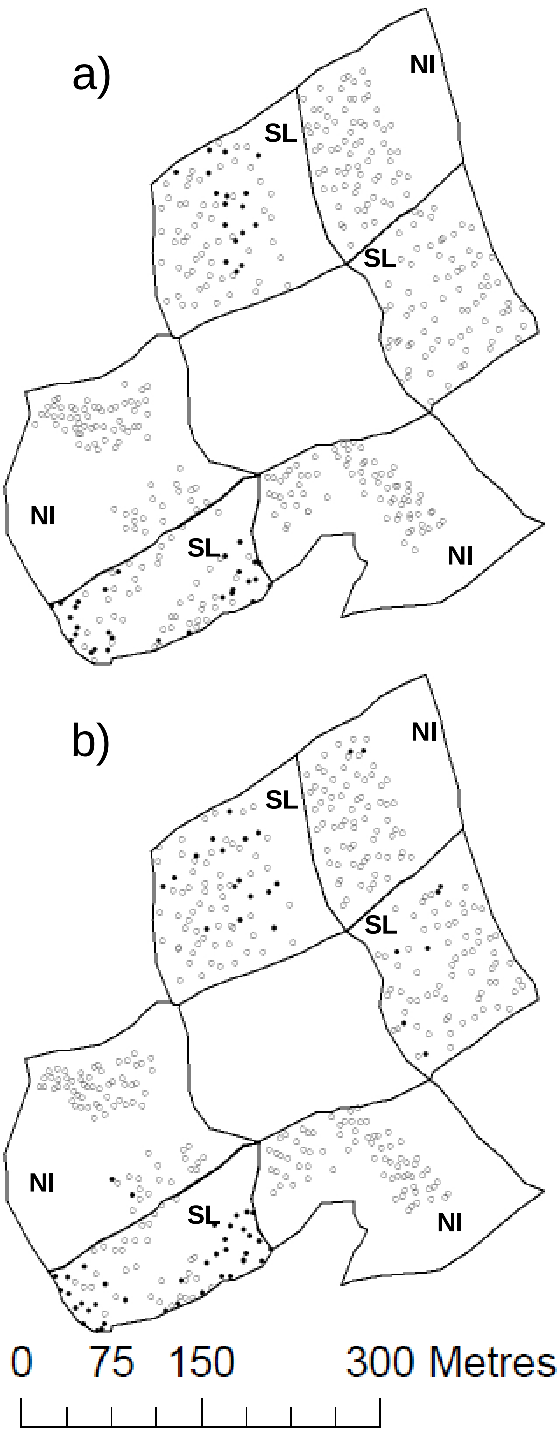
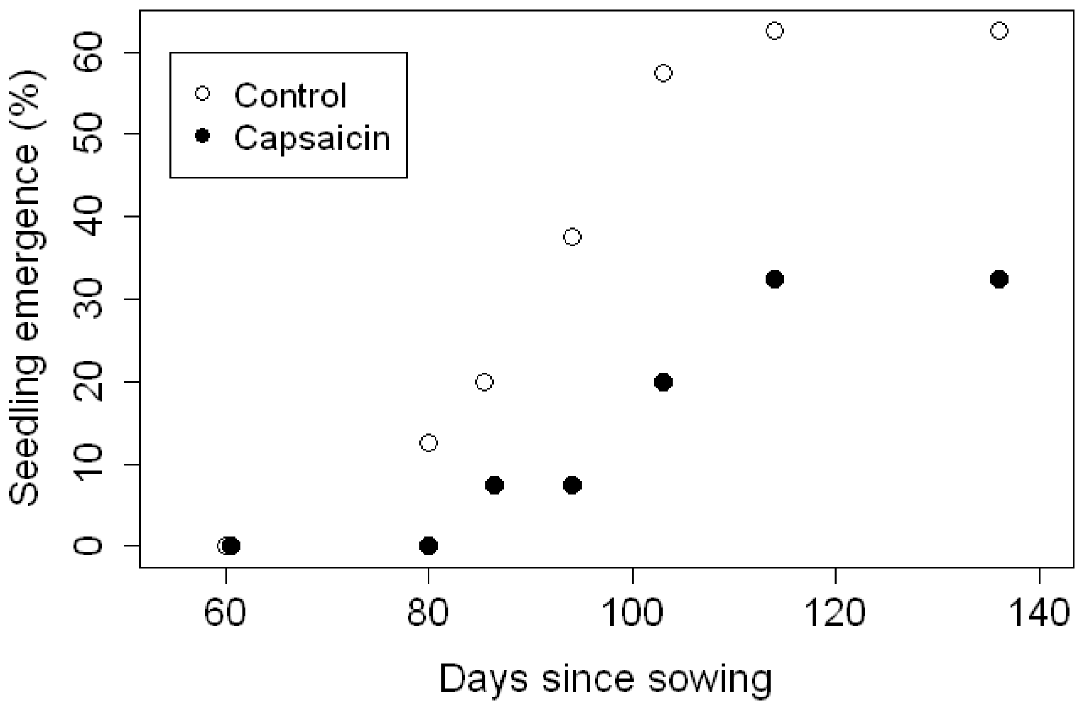


Figure 4


Control
Capsaicin
Seedling emergence (%)
0
10
20
30
40
50
60
60
80
100
120
140
Days since sowing