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Tree regeneration under high levels of wild ungulates: The use of chemically vs. physically-defended shrubs

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ABSTRACT

Wild ungulate populations have increased dramatically in the last decades, limiting tree regeneration. However, how different types of shrubs (chemically vs. physically-defended) act as seedlings facilitators under different types of ungulate damage (browsing or rooting) remains largely unknown. Here, we integrate both biotic and abiotic stress to assess seedling survival in three microsites [open, under chemically-defended (aromatic) shrubs and under physically-defended (spiny) shrubs]. We studied seedling survival of a Mediterranean oak (*Quercus pyrenaica*) for two contrasting levels of abiotic stress (dry vs. wet growing seasons) in environments where deer (Cervidae) and wild boar (*Sus scrofa*) are abundant. After the first summer 24.7% of seedlings were still alive in a wet year whereas only 9.0% seedlings survived in a dry year. Seedling survival was higher under shrub cover, independently of the annual weather conditions and the shrub type. Shrubs, on average, reduced seedling mortality by ungulates approximately 75% in a wet year and only 50% in a dry year due to the greater and earlier impact of browsers (deer) in drier years, when preferred food (green grass) is scarce. Physically-defended shrubs prevent wild boar damage better than other microsites, reducing 35–59% boar damage in comparison to other types of shrubs and 70–77% in comparison to open microsites and, therefore, serve as good nurse shrubs in environments where wild boar are abundant. Physically-defended shrubs also worked well as defense against browsers at low abiotic stress (wet years) but diminished its efficiency in comparison to chemically-defended shrubs at high abiotic stress due to the greater browsing activity of deer on spiny shrubs in dry years. Thus, we recommend the use of chemically-defended shrubs as seedling protectors against browsers. Restoration efforts (e.g. reforestation) under high level of ungulates should take into account the type of ungulate damage (browsing vs. rooting) and the predominant type of shrub mechanism against herbivores (chemical vs. physical) to use shrub cover more efficiently in future restoration practices.

1. Introduction

Territories with a long history of human occupation have left many degraded areas of forest land as a result of an intense exploitation (overgrazing, repeated burning, deforestation, etc.; Le Houérou, 1993; Blondel and Aronson, 1999; Valbuena-Carabaña et al., 2010). In these degraded areas, restoration work (e.g. reforestation) is particularly necessary to accelerate the recovery of the ecological processes and their sustainability (SER, 2004). Despite the great economical and environmental effort in forest restoration worldwide (FAO, 2012), many reforestation practices have failed, especially in harsh environments with stressful abiotic (e.g. water deficit) or biotic conditions (e.g. ungulate pressure; Castro et al., 2004). Alternative techniques of forest restoration should come from studies which are strongly based on natural regeneration patterns to improve both their efficacy and efficiency.

In the last decades, populations of wild ungulates have increased dramatically in the Northern Hemisphere (Kuiters et al., 1996; Gordon et al., 2004; San Miguel et al., 2010), particularly deer (Cervidae) and wild boar –*Sus scrofa*- (Gill, 1990; Massei et al., 2011). Many studies have shown that prolonged herbivory of wild ungulates limits tree recruitment (Anderson and Loucks, 1979; Rooney and Waller, 2003; White, 2012). In fact, ungulate browsing has become one of the main factors constraining seedling performance in many ecosystems (Gill, 1992; Côté et al., 2004). However, most studies have usually neglected other types of ungulate damage such as trampling or rooting (e.g., wild boar). Wild boars are among the most widely distributed mammals in the world and are increasing dramatically in range and numbers (Massei et al., 2011). Their high impact on tree regeneration, especially by rooting up the seedlings, hinders the effectiveness of restoration efforts and is becoming a major problem for managers. This is especially evident for *Quercus* seedlings (widely used in reforestation worldwide; Stange and Shea, 1998; Madsen and Löf,

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2005; Rey-Benayas et al., 2005) whose acorns remain attached to the seedling and are eagerly searched by boars. Thus, reforestations are suffering great plant losses as a result of two different ungulate effects, heavy browsing and rooting.

Seedling establishment is considered the most critical stage in the regeneration process of many trees (Clark et al., 1999). Many field studies have shown a spatial association of seedlings and shrubs that suggests a facilitative effect in which the shrub ameliorates the seedling environment (abiotic amelioration) or protects the seedling from herbivory (Callaway, 1992, 1995; Castro et al., 2004; Smit et al., 2007). In contrast, dense shrub cover may compete with the seedling, causing the death of the reforested plants or a strong reduction in their growth (Savill et al., 1997). It has been suggested that the proportion of facilitative and competitive interactions depends on the weather conditions (abiotic stress) of each particular season (e.g. water deficit; Callaway, 1992). This has led to a debate on how shrubs and tree seedlings interact along abiotic stress gradients, giving support (Pugnaire and Luque, 2001; Callaway et al., 2002; Maestre et al., 2009) or not (Armas and Pugnaire, 2005; Freestone, 2006) to the Stress Gradient Hypothesis (SGH). Following SGH predictions for a highly variable climate such as the Mediterranean, with wet and dry years, we expect shrubs to shift towards a more competitive effect in wet years (lower abiotic stress). However, how the biotic component (ungulate damage) inserts in this hypothesis and how both sources of stress (biotic and abiotic) interact remains largely unknown and deserves further attention (Smit et al., 2009b).

Shrubs differ in their palatability and, thus, are more or less preferred by ungulates (Perea et al., 2008; Miranda et al., 2011), which leads to different probabilities of animal damage on the seedlings growing beneath. Shrubs protect themselves from animals and, consequently, the seedlings growing beneath, through two main mechanisms: chemical defenses (secondary compounds that make the plant unpalatable or toxic) and physical traits (e.g. spines that prevent animals from accessing the green tissue). In many plant species one of the mechanisms usually predominates over the other (Crawley, 1983; Howe and Westley, 1988; Agrawal and Fishbein, 2006) and studies should therefore distinguish between chemically and physically-defended shrubs to test for possible differences in their protective effect on seedlings against different types of ungulate damage (e.g. browsing vs. rooting). Although many chemical compounds and physical traits are common to multiple plant species, there are usually high levels of specificity in the effects of plants on a particular herbivore (Van Zandt and Agrawal, 2004; Kessler and Halitschke, 2007).

In this study, we examine seedling performance of a Mediterranean oak species (*Quercus pyrenaica* Willd.) under chemically and physically-defended shrubs to test their possible differences in the effectiveness as facilitators against wild ungulates (deer and wild boar) under two levels of abiotic stress (two contrasting meteorological years). We also transplanted oak seedlings to open microsites to evaluate the real effect of shrubs (either chemically or physically defended) on seedling survival, considering both biotic and abiotic mechanisms of shrub facilitation. This will help to assess whether shrubs act as facilitators or competitors for seedlings depending on the predominant shrub mechanism against ungulates (chemical vs. physical) and the annual abiotic conditions (wet vs. dry year).

2. Material and methods

2.1. Study area

The study area is located in Cabañeros National Park, within the mountain range "Montes de Toledo", Central Spain (39°23′47″N; 4°29′14″W) at 700–1100 m a.s.l. The climate is Mediterranean with a highly variable precipitation (mean annual rainfall of 541 mm) and 3–4 months of summer drought (June-September). Temperatures are high in summer and cold in winter with frequent frosts from December to March. Mean annual temperature is 15.2 °C. Soils are poor in nutrients and acid (pH $\approx$ 5.2) with a lithological substrate of quartzites and slates.

The vegetation is dominated by sclerophyllous and semideciduous oak forests and woodlands (*Quercus ilex*, *Quercus suber*, *Quercus faginea* and *Quercus pyrenaica*). The understorey is dominated mostly by evergreen shrubs (*Cistus*, *Rosmarinus*, *Erica*, *Phillyrea*, *Rubus*, *Daphne*, *Cytisus*) and some annual herbaceous species (mainly grasses). Evergreen shrubs constitute an important and permanent source of low-medium food quality for herbivores, worse than green grass but better than dry grass (San Miguel et al., 1999). Wooded grasslands (dehesas) are common in the low part of the National Park. Grass dries up every year in spring or early summer (late April-early July) depending on the annual weather conditions. Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are the main wild ungulates in this area. Roe-deer (*Capreolus capreolus*) are scarce and there are no domestic ungulates grazing in this National Park. Current densities of red deer are 15–20 individuals per km^2 (data obtained from the National Park). This species browses more intensely in winter (December–March) and summer (July–September) when no alternative high-quality food is available (green grass or acorns). Densities of wild boar are variable but usually above 8 individuals per km^2 (data based on captures from a close State Property –Quintos de Mora-). Currently, wild ungulates, in this area, have no natural predators and their populations, in this National Park, are regulated mainly by capturing the animals alive in large exclosures and selling them to private country estates. Hunting (shooting) is forbidden in the public properties of this National Park.

2.2. Study sites and species

Experiments were conducted only in oak forests where *Quercus pyrenaica* was the dominant tree species. We selected the *Quercus pyrenaica* forests in the Brezoso area, in the East part of the National Park (39°20′05″N; 4°21′17″W), covering approximately 840 ha of flat slopes (<2%). *Quercus pyrenaica* is a semideciduous oak species, native to Southwestern Europe and Northwestern Africa, that can re-sprout after being damaged (e.g., by light browsing; Ruiz de la Torre, 2006). Currently, regeneration of *Quercus pyrenaica* in Central and Southern Spain (including this National Park) is very poor, mostly due to high ungulate densities (Gómez et al., 2003; Plieninger et al., 2010). The understorey of these *Q. pyrenaica* forests is composed mainly by the following shrub species: *Rubus ulmifolius*, *Rosmarinus officinalis*, *Erica arborea*, *Erica scoparia*, *Lavandula pedunculata*, *Thymus mastichina*, *Crataegus monogyna*, *Rosa* sp. and *Daphe gnidium*. Among these shrub species, *Rubus ulmifolius* (Rosaceae) has low levels of chemical defenses against herbivores (Cristobal, 2006; Miranda et al., 2011). However, this species has thorny stems and prickly leaflets that act as a physical defense against herbivores. This species was very common in the study site and was selected as the physically-defended shrub (hereafter, P). Conversely, *Rosmarinus officinalis* is a non-palatable shrub, which produces aromatic compounds, typical of the Labiatae family, as a chemical defense against herbivores (Dietz et al., 1962; Gershenzon and Croteau, 1991). This species is an unarmed shrub, very common in the study site, and was selected as the chemically-defended shrub (hereafter, C). Both *Rubus* and *Rosmarinus* are evergreen and light-demanding shrubs, but *Rubus* usually grows on microsites with more humidity. For the purpose of this study we always selected isolated individuals with similar height (0.70–1.25 m) although they can also