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Do shrubs facilitate oak seedling establishment in Mediterranean pine forest understory?

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ABSTRACT

Shrubs have been shown to facilitate tree seedling establishment in open Mediterranean ecosystem habitats, but their effects in forests have been much less explored. We investigated the role played by shrubs in seedling emergence, survival and growth for two co-occurring oak species – *Quercusilex* and *Quercuspubescens* – in the understory of clear Aleppo pine stands (10 m^2/ha). Acorns of both species were sown in two sites in South-East France that contrasted in terms of former land-use (pastoral *vs* agricultural), soil thickness (shallow *vs* deep) and type of understory (shrubs + grass *vs* only shrubs). Oak seedlings had a higher survival and growth on the former agricultural site with deeper soil. In general, the more stress-tolerant *Q. ilex* performed better than *Q. pubescens*. In the harsher site, seedling survival decreased with grass cover but increased with shrub cover. Shrub and grass cover decreased seedling diameter and had no effect on seedling height. In the more fertile site, shrub cover had no influence on seedling survival but had a species-specific effect on seedling growth: shrubs mostly competed with *Q. ilex* but ameliorated *Q. pubescens* growth, leading to changes in the two species performance ranking at high shrub cover. We conclude that shrubs can act as nurses for oak seedling establishment in pine forest understory, particularly in harsh conditions and for stress-intolerant species. In harsh conditions, shrub cover should be factored in as a way to promote pine forest diversification toward mixed pine–oak stands.

1. Introduction

Millennia of intensive and diverse anthropogenic pressures have shaped forest composition and distribution in the Mediterranean Basin (Blondel, 2006). Since the 19th century, the northern rim of the Mediterranean Basin has undergone strong rural abandonment (Debussche et al., 1999), leading to the expansion of the pioneer Aleppo pine – *Pinus halepensis* Mill. – (Barbero et al., 1990; Debussche et al., 1999). With the course of forest succession, Aleppo pine is expected to be replaced by Mediterranean oaks in most sites (Barbero et al., 1990; Zavala et al., 2000). However, oaks often struggle to regenerate, and oak seedling establishment rates are very low due to numerous factors that hamper the regeneration process. These factors include the lack of close seed sources (Gómez-Aparicio et al., 2009; González-Moreno et al., 2011; Mendoza et al., 2009) and efficient dispersal vectors (Gómez, 2003; Gómez et al., 2007), and after seed arrival, seed predation by rodents and wild boars which can be very high (Puerta-Piñero, 2010). Microsite suitability for seedling emergence, growth and survival is also a major factor (Espelta et al., 1995; Mendoza et al., 2009; Pulido and Díaz, 2005).

As forest managers look to facilitate forest adaptation to climate change, favoring the transition toward mixed pine–oak stands is increasingly being advocated as a way to increase forest resilience to wildfires (e.g. Pausas et al., 2004; Vallejo et al., 2012) by taking advantage of oak resprouting abilities (Keeley, 1986; Puerta-Piñero et al., 2012). Seed limitations and predation can be overcome by artificially sowing and protecting acorns, but a good knowledge of favorable microsites is required. Several studies have shown that dense Aleppo pine stands severely limit oak establishment (Gómez-Aparicio et al., 2009; Maestre et al., 2003; Sheffer et al., 2013). Thinning dense stands has thus been recommended to increase the probability of oak seedling establishment (Gavinet et al., 2015; Prévosto et al., 2011). However, thinning can also promote colonization of the pine understory by other spontaneous species (Royo and Carson, 2006), which may offset the positive effects of canopy opening (Beckage et al., 2005). Understory

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vegetation is most often considered as competing with target-tree seedlings (Balandier et al., 2006; Paquette et al., 2006; Royo and Carson, 2006) including oak species (e.g. Lorimer et al., 1994), so many forest managers try to suppress it by mechanical or chemical means in an effort to enhance target species establishment (McCarthy et al., 2011). However, competitive interactions between plants are expected to decrease in harsh sites such as dry areas, where facilitation can play a greater role (Bertness and Callaway, 1994; He et al., 2013). Several studies in Mediterranean conditions have shown positive effects of shrubs on tree seedling establishment, including oaks, compared to open areas (Castro et al., 2004; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006; Rousset and Lepart, 1999). However, there has been much less investigation into the effects of shrubs in the understory of Mediterranean forest stands. The presence of a canopy, by reducing light availability but also by changing other environmental factors (e.g. microclimate, soil moisture), can influence the outcomes of shrub–seedling interaction (Muhamed et al., 2013b). It has been shown that plant–plant interactions are highly context-dependent and also species specific, target species responses to neighbors depending in particular of their stress tolerance and competitive abilities (Liancourt et al., 2005; Michalet, 2007; Saccone et al., 2009). Further experiments assessing the effects of understory vegetation on oak seedling establishment is needed in order to improve understanding of the factors driving pine–oak succession and propose appropriate forest management methods.

Here we examine the effect of understory vegetation that spontaneously developed after Aleppo pine overstory thinning on the establishment of the two main oak species in Southern France, the holm oak (*Quercus ilex* L.) and the downy oak (*Quercus pubescens* Willd.). Among the two species, holm oak is considered more drought-tolerant while pubescent oak dominates mature forests in sites with higher precipitations or deeper soils (Barbero et al., 1990; Migliorетti, 1987; Zavala et al., 2000). In general, a trade-off between drought and shade tolerance is expected (Niinemets and Valladares, 2006), which explains the findings that drought intolerant-shade tolerant species are more facilitated (Gómez-Aparicio et al., 2004; Liancourt et al., 2005; Pages and Michalet, 2006). However, holm oak has also been shown to be also highly shade-tolerant (Sánchez-Gómez et al., 2008) probably thanks to a conservative strategy which allows this species to tolerate low levels of both light and water by reducing losses and demands for resources (Sack et al., 2003). Field experiments in the Mediterranean indeed found a higher tolerance of holm oak to deep shade compared to pubescent oak (Prévosto et al., 2011, 2016). Thus, the relative importance of facilitation and competition for the two oak species is far from being easily predictable. To assess this, we conducted a sowing experiment in two Mediterranean pine forests with contrasting soil fertility conditions and land-use histories, and tested for relationships between understory cover and oak seedling emergence, survival and growth. We hypothesized that

(i) shrub cover can facilitate oak seedling establishment,
(ii) the less stress-tolerant *Q. pubescens* would benefit more from presence of neighbor shrubs.

2. Material and methods

2.1. Experimental sites and vegetation treatments

Both experimental sites are located in South-Eastern France. The first site is located in Barbentane ('Barbentane' site; 43°5′N–4°4′W), on a gentle north-oriented slope at an altitude of 105 m. Mean annual temperature is 14 °C and mean annual rainfall is 689 mm (1961–1996, Avignon weather station, Météo-France). During the experiment, precipitations were below the mean in the first two years (517 and 383 mm) and above during the third year (946 mm). Before the experiment, the vegetation was dominated by 90-year-old Aleppo pine stands that had naturally established on former grazing land, with a heterogeneous shrub layer (*Quercus coccifera* L., *Quercus ilex* and *Buxus sempervirens* L.) and a ground layer dominated by the grass *Brachypodium retusum* (Pers.) Beauv. The soil iscalcareous and shallow with loamy texture, high stone amount, and a mean depth of 15 cm. The whole Aleppo pine stand was thinned down in 2003 to a basal area of 12 m^2/ha and a density of 210 trees/ha. Light records in July 2005 using solarimeter tubes (300–3000 nm, Delta-T Device) showed a light transmittance of 70%. Different soil and understory vegetation treatments were applied in winter and spring 2005. These treatments were originally designed to enhance natural pine regeneration and resulted in different understory vegetation development patterns (see Prévosto and Ripert, 2008 for further details on the treatments). Treatments were replicated in four 34 × 82 m plots containing each ten 14 × 14 m subplots with different vegetation treatments.

The second site is located in St-Mitre-les-Remparts ('St Mitre' site, 43°4′N; 5°0′W) about 80 km south of the first site, on a flat area at an altitude of 130 m. Mean annual temperature is 14.5 °C and mean annual rainfall is 550 mm based on historical records (1961–2010, Istres weather station, Météo France). During the 3 years of the experiment, precipitations were higher than the mean with 779, 697 and 661 mm. The vegetation is dominated by 60-year-old Aleppo pine stands that had naturally established on former agricultural fields (terraces) with a scarce understory mainly composed of shrubs (*Quercus coccifera*, *Quercus ilex* and *Cistus albidus* L.). The soil is calcareous with sandy-loam texture, a low stone load, and a mean depth of 40 cm indicating higher soil fertility than in the previous site. The Aleppo pine stand was thinned down to 10 m^2/ha (density 197 trees/ha) in 2006 in four 25 × 25 m plots. Light records in July 2008 using solarimeter tubes (300–3000 nm, Delta-T Device) showed a light transmittance of 52%. No soil or understory vegetation treatments were applied.

2.2. Oak introduction by acorn sowing

Acorns of *Q. pubescens* and *Q. ilex* were introduced in autumn 2005 at Barbentane and autumn 2007 at St Mitre. Acorns were collected in the autumn of these same years, on several sites of similar ecological conditions and using several trees per site for each oak in order to encompass intraspecific variation. Non-viable acorns were eliminated by the floating method and visual screening. Viable acorns were then stored in moist conditions until being sown in late autumn. At each sowing point, three acorns of the same species were laid flat in a small hole (10 cm × 10 cm, 4 cm deep), covered with 2 cm of soil, a wire mesh (same dimensions, 0.6 cm mesh size, to prevent predation by small rodents) and covered by a further 2 cm layer of soil. At Barbentane, 100 sowing points of each oak species were introduced per plot, resulting in a total of 400 sowing points (1200 acorns) per oak. At St Mitre, 52 sowing points of each oak were introduced per plot, resulting in a total of 208 sowing points (624 acorns) per oak. At both sites, sowing points were arrayed in rows, alternating *Q. ilex* and *Q. pubescens*. The distance between rows was 2.5 m and between sowing points in the row 3 m at Barbentane, 2 m and 1 m at St Mitre. Plots were fenced to limit herbivory and prevent damage from wild boar.

2.3. Vegetation monitoring

Emerged seedlings were counted at each sowing point in the first spring after acorn introduction and then every year, in winter, after the end of the vegetation season until they reached 3 years