



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 – *Quercus ilex* and *Quercus pubescens* – in the understory of clear Aleppo pine stands (10 m²/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.

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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 (Muhammed 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; Miglioretti, 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 is calcareous 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 m²/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 m²/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

old. Emergence was measured as number of seedlings emerged at the first census date. Survival was measured as number of alive seedlings along the years. Apparently dead seedlings that later resprouted were counted as alive. Dimensions (height and stem basal diameter) of the seedlings at each sowing point were recorded after 3 vegetation seasons. For further analyses, the dimensions of each sowing point's tallest seedling were taken into account.

Understorey shrub and grass cover were assessed at emergence and 3 years after oak introduction at each sowing point. Cover was visually estimated using a 25 cm-radius hoop centered on the sowing point via a method derived from the Braun-Blanquet abundance/dominance method: 1 = <1%, 2 = [1–5%], 3 = [5–25%], 4 = [25–50%], 5 = [50–75%], 6 = [75–100%]. For emergence analysis, classes were pooled in order to assure a sufficient number ($n > 20$) in a given class. For survival and growth analyses, we used the mid-point of each class 3 years after emergence. At Barbentane, both herbaceous and woody species developed, whereas only woody species colonized the understorey at St Mitre (Fig. 1). This can be explained by different initial floristic compositions due to different land-use histories (grazing in Barbentane vs agriculture in St Mitre) and surrounding landscape seed sources.

2.4. Data analysis

In each site, the effects of species identity, understorey vegetation cover and their interaction on seedling emergence was analyzed at the sowing point levels using Generalized Linear Models with a Poisson distribution. The effect of these factors on oak seedling survival was analyzed using Cox mixed models with plot as random factor (R package coxme). Cox models estimate individual seedling time-to-death according to factors, taking into account censored data, and give estimates of mortality risk according to factor values (Cox, 1972). The effects of species identity, understorey vegetation cover and their interaction on oak seedling dimensions (height and basal diameter) were analyzed using linear

mixed models after log-transforming the response variables if necessary to satisfy normality and homogeneity of the variances. The final models presented in the figures to this paper were obtained by backward selection of significant factors. All statistical analysis was performed using R software (3.2.1).

3. Results

3.1. Seedling emergence and survival

Total emergence was lower at Barbentane (68% of introduced emerged acorns) than at St Mitre (88%). Emergence was negatively affected by grass cover at the Barbentane site (Table 1) but not by shrub cover or species identity.

Seedling survival after 3 years was lower at Barbentane (29% of emerged acorns) than at St Mitre (79%). This result hold when considering only survival without neighbors (grass and shrub cover <5%). At Barbentane, seedling survival was affected by species identity and vegetation cover but not by species identity × vegetation cover interaction (Table 2). Survival was over two-fold higher for holm oak (40%) than downy oak (19%) and for both species was positively affected by shrub cover and negatively affected by grass cover (Tables 1 and 2; Fig. 2), whereas at St Mitre, neither species identity nor understorey cover had any effects on survival (Table 2; Fig. 3).

3.2. Seedling dimensions

Seedling mean diameter was similar at Barbentane (3.0 ± 0.01 mm) than at St Mitre (2.9 ± 0.1 mm). At Barbentane, diameter was negatively affected by both grass and shrub cover, with no difference between the two species (Table 3; Fig. 4). At St Mitre, holm oak diameter was higher than downy oak diameter, but was negatively affected by shrub cover (Table 3; Fig. 4), whereas downy oak diameter was unaffected by shrub cover.

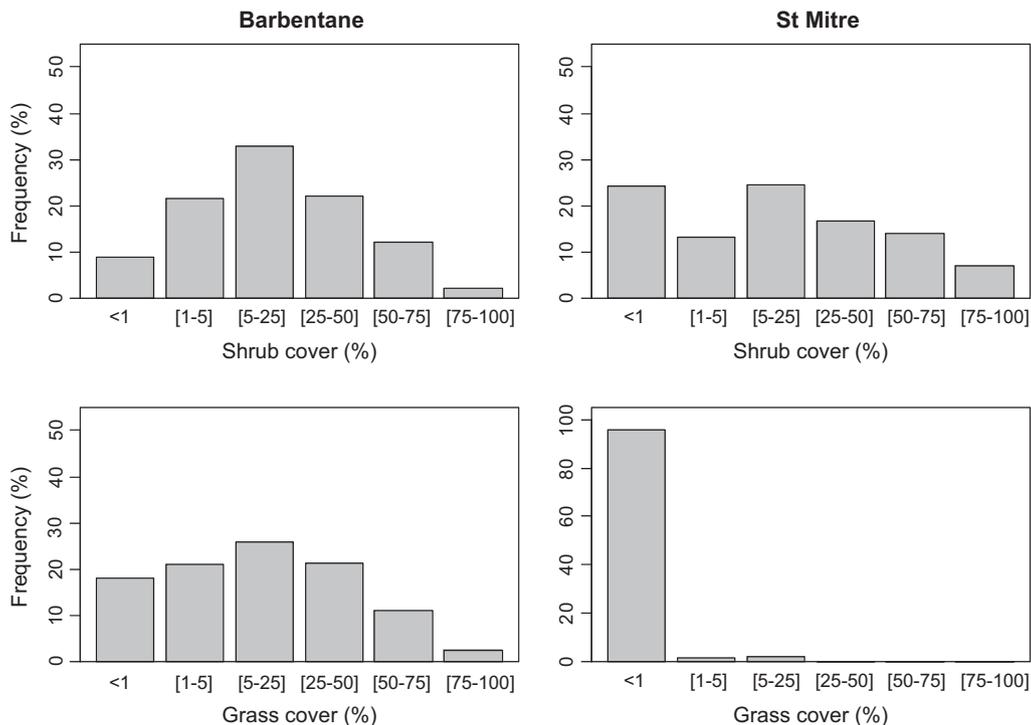


Fig. 1. Understorey vegetation development in the two sites three years after introducing oaks.

Table 1

Results of GLM testing for species identity and understory vegetation cover effects on seedling emergence. Significant p-values at $p < 0.05$ are indicated in bold.

	Df	Likelihood ratio χ^2	p-Value
<i>Barbentane</i>			
Sp	1	0.02	0.89
Shrub cover	2	4.62	0.10
Grass cover	2	16.57	<0.001
Sp \times shrub cover	2	2.10	0.35
Sp \times grass cover	2	1.29	0.52
<i>St Mitre</i>			
Sp	1	0.11	0.74
Shrub cover	2	0.02	0.98
Sp \times shrub cover	2	0.03	0.98

Table 2

Results of Cox mixed model testing for species identity and understory vegetation cover effects on seedling survival. Significant p-values at $p < 0.05$ are indicated in bold.

	Df	χ^2	p-Value
<i>Barbentane</i>			
Sp	1	81.25	<0.001
Shrub cover	1	55.13	<0.001
Grass cover	1	18.39	<0.001
Sp \times shrub cover	1	0.02	0.88
Sp \times grass cover	1	0.78	0.38
<i>St Mitre</i>			
Sp	1	0.02	0.88
Shrub cover	1	1.74	0.18
Sp \times shrub cover	1	0.89	0.2

Seedling mean height was higher at St Mitre (14.1 ± 0.4 cm) than at Barbentane (11.2 ± 0.3 cm). At Barbentane, holm oak seedlings were taller than downy oak seedlings, with no effect of understory vegetation on either species (Table 3; Fig. 5). At St Mitre, seedling height was affected by species identity, shrub cover and their interaction. There was a positive effect of shrub cover on seedling height in both oak species, but this effect was stronger for downy oak. As a result, downy oak had lower dimensions than holm oak under low shrub cover but similar dimensions under high shrub cover (Fig. 5).

4. Discussion

4.1. Understory vegetation and site effects on seedling emergence and survival

The conditions at the Barbentane site appeared more stressful for seedlings, which showed a much lower emergence and survival

than at St Mitre, in particular for downy oak (19% vs 79% survival). These more stressful conditions are probably the result of lower precipitations during the two first years combined with highly constraining edaphic conditions due to a rocky and shallow soil.

Seedling emergence is largely dependent on seed stores (Gómez, 2004; Long and Jones, 1996) but can also be affected by the microclimate conditions created by co-occurring vegetation cover. At Barbentane, oak seedling emergence was negatively affected by grass cover but not by shrub cover. Similarly, Gordon and Rice (2000) found that herbaceous species inhibited *Quercus douglasii* emergence, which they linked to an early depletion of soil water by herbaceous species. Conversely, Pérez-Ramos et al. (2012) found that tree cover favored *Quercus suber* emergence, an effect that they attributed to higher humidity.

Understory vegetation influenced seedling survival, but only in the less fertile site (Barbentane) and with contrasted effects depending on type of vegetation: positive for shrubs and negative for grass. The positive effect of shrubs on survival is probably due to both direct alleviation of stress by microclimate amelioration and photoprotection (Gómez-Aparicio et al., 2005) and indirect interactions by suppressing grasses. Indirect interactions mediated by herbs have already been outlined as important mechanisms of facilitation by shrubs in Mediterranean ecosystems (Caldeira et al., 2014; Cuesta et al., 2010; Kunstler et al., 2006). The dominant herb in our study was the perennial grass *Brachypodium retusum*, which has been reported as particularly efficient in depleting soil water (Casas and Ninot, 2007) and detrimental to woody seedling establishment (Amat et al., 2014; Maestre et al., 2004). Different herbaceous species (in particular graminoids vs non-graminoids) can have contrasting impact on soil water and microclimate conditions, which explains why positive effects of herbs on tree seedlings have also been reported (e.g. Maestre et al., 2001). However, in this study shrub cover explained only 1.4% of grass cover variation, thus grass suppression was not the only mechanism explaining improved survival under shrubs.

In more favorable conditions (St Mitre), understory shrubs had no influence on seedling emergence and survival. Similarly, Muhamed et al. (2013b) found that understory shrubs had a more positive effect on oak seedling survival at a dry site than at a wet site in South West France. These results are consistent with the 'stress-gradient hypothesis' (Bertness and Callaway, 1994) that positive interactions increase under stressful conditions. Under temperate conditions, understory cover is mostly considered as competing with tree seedlings (Balandier et al., 2006; Parker et al., 2009; Royo and Carson, 2006), but under Mediterranean conditions where the summer drought constraint is high, shrubs may act as facilitator. Other studies in the Mediterranean have found a

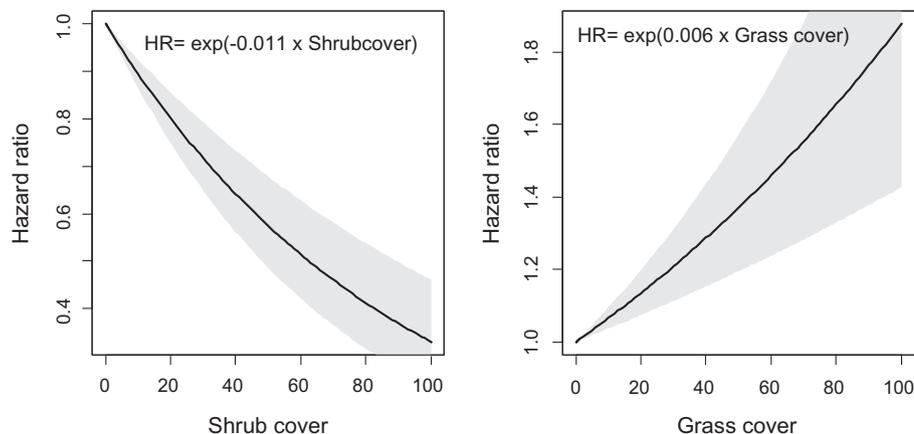


Fig. 2. Hazard ratio (HR) of seedling mortality risk as a function of shrub and grass cover for both species at the Barbentane site (equations from backward selection of significant terms in the model shown in Table 1). Mortality risk with no shrub or grass cover is taken as reference (HR = 1). No effect of shrub cover was detected at St Mitre.

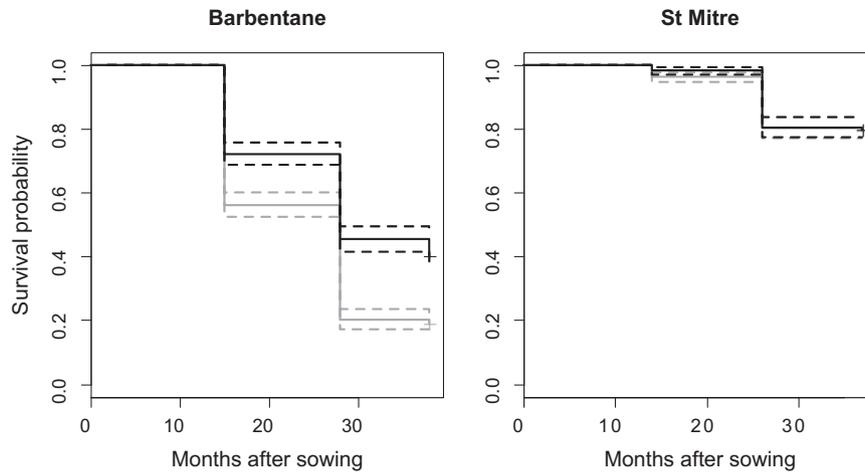


Fig. 3. Seedling survival probability as a function of species identity and time. Black lines plot *Quercus ilex* and grey lines plot *Quercus pubescens*. Dashed lines are 95% confidence intervals.

Table 3

Results of linear mixed models testing for species and understory vegetation effects on seedling dimensions. Significant p-values at $p < 0.05$ are indicated in bold.

	Diameter			Height		
	Df	F-value	p-Value	Df	F-value	p-Value
<i>Barbentane</i>						
Sp	1	0	0.99	1	10.3	0.002
Shrub cover	1	3.7	0.05	1	2.44	0.12
Grass cover	1	8	0.005	1	0.02	0.87
Sp × shrub cover	1	1.05	0.31	1	0.6	0.45
Sp × grass cover	1	1.14	0.29	1	0.9	0.34
Residuals	156			156		
<i>St Mitre</i>						
Sp	1	134.9	<0.001	1	163.6	<0.001
Shrub cover	1	3.35	0.07	1	33.4	<0.001
Sp × shrub cover	1	23.7	<0.001	1	12.6	<0.001
Residuals	380			380		

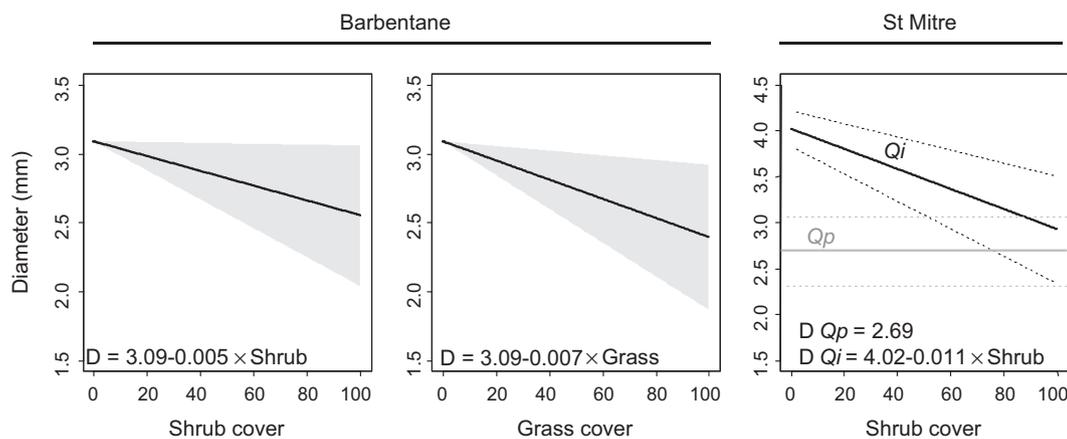


Fig. 4. Seedling diameter as influenced by species identity and understory vegetation cover. Equations from backward selection of significant terms shown in Table 3. Left: Barbentane site, no species differences, grey area represents 95% confidence intervals, R^2 of the whole model = 9.5%. Right: St Mitre site, black lines plot *Quercus ilex* (Q_i) and grey lines plot *Quercus pubescens* (Q_p), dashed lines are 95% confidence intervals, $R^2 = 33.3\%$.

positive effect of understory shrub cover on oak regeneration, either through observation of natural regeneration (Martín-Alcón et al., 2015; Vayreda et al., 2013) or experimental introduction of acorns as was the case here. Positive effects of understory shrubs have even been found for the regeneration of highly light-demanding species like pine (Rodríguez-García et al., 2011), although negative effects on pine saplings have also been reported

(Martín-Alcón et al., 2015). However, the degree of canopy opening in studied stands can also influence understory shrub effects (Martín-Alcón et al., 2015; Muhamed et al., 2013a, 2013b) because it creates different microclimatic conditions in the understory (Gavinet et al., 2015). For instance, in the understory of *Pinus nigra* stands in north-east Spain, Martín-Alcón et al. (2015) found that positive shrub effects on marcescent oak seedling density

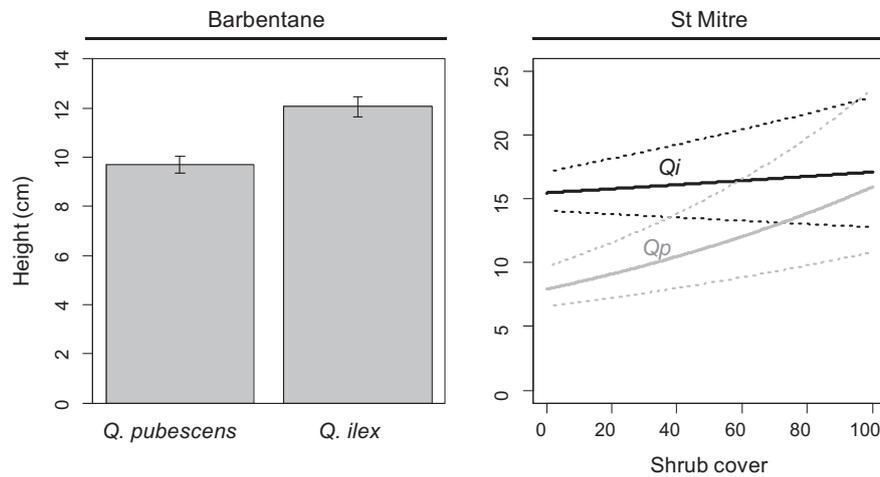


Fig. 5. Seedlings height as influenced by species identity and understory vegetation cover. Left: Barbantane site, no effect of understory vegetation cover, $R^2 = 16.2\%$. Right: St Mitre site, black lines plot *Quercus ilex* (Qi), grey lines plot *Quercus pubescens* (Qp), dashed lines are 95% confidence intervals, $R^2 = 44.1\%$.

decreased or became negative at high shrub cover in overstory gaps. In denser Mediterranean forests, understory shrubs may have a more negative impact on tree regeneration. Here, we compared shrub effects in the understory of clear Aleppo pine stands with a similar basal area (10–12 m²/ha), but degree of light transmittance was higher at Barbantane (70%) than at St Mitre (52%), probably due to different tree heights or crown conformation linked to different soil fertility levels. Despite similar climates, different soil characteristics and land-use histories thus play a key role in determining site-level stress conditions and plant–plant interaction outcomes. This heterogeneity is particularly high in Mediterranean landscapes (Blondel, 2006) but should be taken into account, along with macroclimate data, when studying plant–plant interaction variation across stress gradients. Despite this heterogeneity, studies to date have mostly found neutral or positive effects of shrubs on broadleaved tree seedling establishment in the understory, in contrast with what is usually found in milder climates.

4.2. Species-specific growth responses to understory vegetation cover

For both species at Barbantane, shrub and grass cover had a negative effect on diameter growth with no effect on height growth, leading to globally lower aboveground growth of seedlings. Several studies in drylands have also found similar ontogenetic conflicts between shrub facilitation for survival and competition for growth (e.g. Miriti, 2006). However, at St Mitre site, shrub cover suppressed diameter growth for *Q. ilex* but not for *Q. pubescens* and stimulated height growth in both species. Shrub cover thus induced an elongation of *Q. ilex* seedlings, probably through lateral shading, change of light quality and/or physical barriers to lateral expansion (Franklin, 2008). In contrast, shrub cover improved the aboveground growth of *Q. pubescens*. Shrub cover thus had a complex impact on aboveground growth, ranging from neutral-to-negative for diameter growth and neutral-to-positive for height growth.

Q. pubescens had lower dimensions than *Q. ilex* at both sites and lower survival rates at Barbantane, confirming that the first species is less stress-tolerant and better adapted to the tested conditions in its young stages. As hypothesized, the growth of the less stress-tolerant species *Q. pubescens* benefited more from the presence of shrubs on the good soils at St Mitre. Shrubs provided favorable microsites for this species, allowing it to reach similar dimensions than *Q. ilex* at high shrub cover. Understory shrubs thus acted as a

“filter” able to change the ranking of the seedlings and potentially alter forest successional trajectories (George and Bazzaz, 1999). In a study on the regeneration of two oak species with similar characteristics, the evergreen *Q. ilex ballota* Samp and the marcescent *Q. pyrenaica* Willd, Madrigal-González et al. (2014) found that shrubs positively influenced the regeneration of the marcescent oak, which led to a shift in the bioclimatic limit between the two oaks along an elevation gradient. This further underlines that shrubs, as a favorable microsite for stress-intolerant oaks, have an important role to play in the maintenance of these species at the margin of their regeneration niche.

Note however that this species-specific growth response to shrub cover was confirmed at St Mitre but not at Barbantane where the two oak species showed similar growth responses to understory vegetation. At Barbantane, oaks experienced higher water stress levels (lower precipitations, lower soil depth with higher stone load and higher grass cover). It has been proposed that when a resource-based stress level is too high for the target species, competition for resources may overwhelm positive effects and a switchback to competition may occur (Michalet et al., 2014). *Q. pubescens* is described as more sensitive to water availability, which restricts its ability to develop in dry areas and/or unfavorable soil conditions. The water stress level reached by this species at Barbantane on shallow soils may have prevented it fully benefiting from shrub shading for its growth. Conversely, at St Mitre with less soil water limitation, the alleviation of above-ground stress by shrubs may have allowed higher gas exchange and growth of *Q. pubescens*.

5. Conclusion

In clear pine forest stands, understory shrubs showed a neutral-to-positive influence on oak seedling survival, whereas grass cover showed a strong competitive effect with oak seedling survival and growth, probably reflecting competition for water in the upper soil layers. Shrub facilitation for survival occurred only in the most stressful site, in line with the stress-gradient hypothesis. However, shrub facilitation for growth occurred only on the more favorable site with deeper soils. Soil characteristics and indirect interactions are particularly important factors to integrate when assessing the change of interaction outcomes along an environmental gradient, especially in Mediterranean areas where soil conditions and landscape history are particularly heterogeneous and can strongly impact the level of effective water stress for seedlings. In the more favorable site, shrubs only facilitated growth of the less stress-

tolerant species *Q. pubescens*, leading to changes in the relative ranking of the two oaks at high shrub cover. Shrubs can thus act as regeneration niches enabling this species to persist in these conditions.

These results highlight that in the Mediterranean context, understory shrubs can act as nurses for oak seedling establishment. This seems more likely to happen in stressful conditions and for less stress-tolerant species. However, further research should be undertaken to investigate more in depth the role of understory shrubs for different sites, target species and canopy cover conditions. Forest managers planning operations should also consider shrubs as an important component of the understory vegetation with a role to play in the transition from pure to mixed pine–oak stands.

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