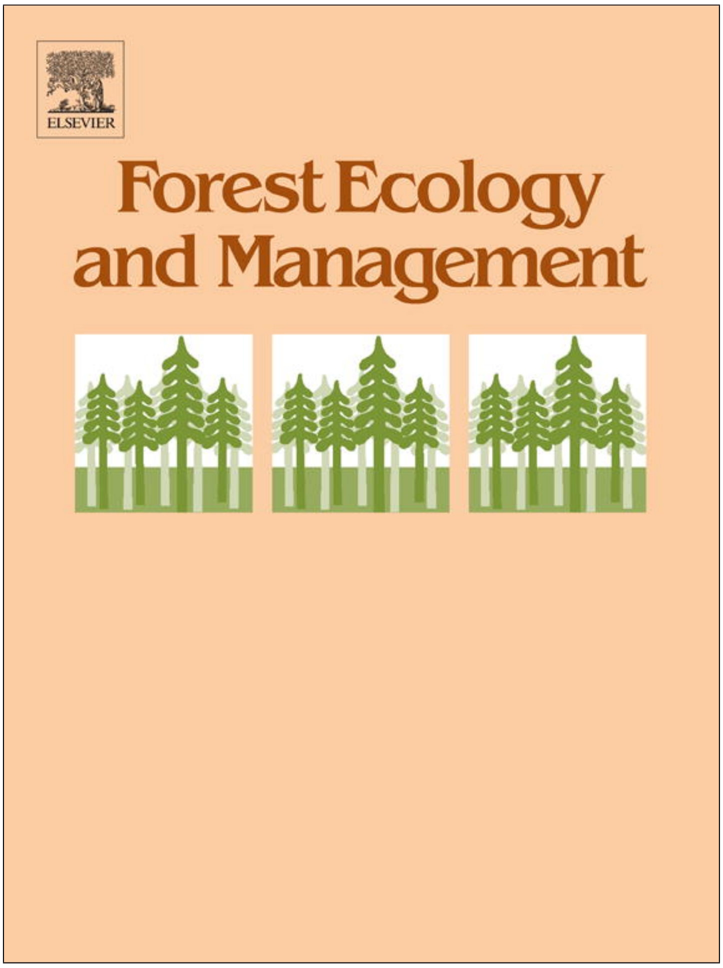

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The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities

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ABSTRACT

Although forest managers are aware of the need to adapt forest management to climate change, this task is still challenging due to the difficulty for predicting local species and communities responses to climate change. The aim of this paper is to focus on the adaptation of sylvicultural techniques to changes in interactions between tree recruitment and understory species due to climate change. A space-for-time design was used in coastal dune forest communities from the south west of France. The study area is a 240 km-long sand strip covered by forest communities with minimal variation in soil conditions along a natural gradient of increasing water stress. We transplanted seedlings of three oak species of contrasting strategies at both the wet and dry ends of the climate gradient, both in forest and gap plots and with and without understory shrubs. We measured Vapor Pressure Deficit in all treatment conditions. We found strong canopy and climate conditions effects on interactions between understory shrubs and oak transplants. Competition was dominant in the forest plots of the wettest site and facilitation in the gap plots of the driest site. Oak survival without shrubs (but not with shrubs) was strongly related to VPD values, which suggests that the positive effect of shrubs in the most stressful conditions was due to decreased atmospheric stress below their canopy. In contrast, we found that understory shrubs/oak seedlings interactions were weakly affected by oak species functional strategies. Our results provide evidence that future oak regeneration management should take into account changes in interactions with understory shrubs due to climate change. In particular, we recommend conserving understory shrubs in the most stressful sites in order to maintain a sufficient oak regeneration for the long term dynamics of coastal oak forest communities under changing climate.

1. Introduction

Together with abiotic conditions and dispersal, plant–plant interactions are known to be crucial drivers of the early establishment of tree seedlings in forest communities (Lortie et al., 2004; Brooker et al., 2009). Since tree species are particularly vulnerable to biotic and abiotic conditions during early life-stages (Kitajima and Fenner, 2000), interactions between understory species and tree recruitments are known to be crucial for tree regeneration and thus forest management (Nambiar and Sands, 1993; Groot, 1999; Balandier et al., 2006; Wagner et al., 2006). Based on the Stress Gradient Hypothesis (SGH, Bertness and Callaway, 1994) competition is more important for tree regeneration in mesic forest communities and facilitation in xeric and other stressful conditions. In particular, there is an increasing interest in using direct facilitation as a tool in ecological restoration of water-stressed ecosystems (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006; Gómez-Aparicio, 2009). Nurse plants may improve soil fertility and/or decrease drought and temperature stress, allowing target tree and shrub seedlings to survive in these severe environmental conditions (Callaway, 1995; Maestre et al., 2009). However, it has also been shown that competition may be intense in water-stressed environments (Davis et al., 1998; Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004; Saccone et al., 2009) and there is still an intense debate on how facilitation and competition vary along water stress gradients (Maestre et al., 2005, 2009; Lortie and Callaway, 2006; Michalet, 2006, 2007; Malkinson and Tielbörger, 2010; Pugnaire et al., 2011).

Gómez-Aparicio et al. (2004) and Michalet (2007) stressed the importance of species traits and strategies of both the nurse and the target species (see also Maestre et al., 2009; Gómez-Aparicio, 2009; Forey et al., 2010). Because of their high allocation to roots, grasses are more likely to compete for water with target species than shrubs (Davis et al., 1998; Maestre et al., 2003; Picon-Cochard et al., 2006; Kunstler et al., 2006; Gómez-Aparicio, 2009). Legumes

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are excellent nurses because of their additional input of nitrogen (Pugnaire et al., 1996; Gómez-Aparicio et al., 2004; Pugnaire et al., 2004). Concerning the strategy of the target species, stress-intolerant species are better candidates for facilitation than stress-tolerant ones, because the benefit of shade (for water availability, air humidity, temperature, photoinhibition) is more likely to compensate its cost for light for the former than for the latter (Liancourt et al., 2005; Saccone et al., 2009; Forey et al., 2010). Finally, it has been stressed the usefulness to distinguish in dry environments atmospheric water stress from soil moisture stress, the former rather inducing facilitative interactions and the latter competitive ones (Michalet, 2007; Saccone et al., 2009; Maestre et al., 2009).

Understanding the role of water stress in driving changes in shrubs-seedlings interactions in forest communities is crucial for predicting how climate change will alter tree regeneration, in particular in southern Europe for which climate change models predict and increase in summer drought (IPCC, 2007). In this study, we aim to focus on the adaptation of sylvicultural techniques to changes in interactions between tree recruitment and understory species due to climate change (Fotelli et al., 2001; Saccone et al., 2009). Because climate change is known to modify interactions among species in plant communities (Brooker, 2006; Saccone et al., 2009), interactions between tree seedlings and understory species are expected to change in forest communities with climate warming and/or drying. We aimed to assess changes in the effects of understory species on tree recruitment in the perspective of climate change in the coastal dune forests of south-western France. In the coastal dune communities of the Aquitaine region, there is a 240 km-long homogeneous sand strip colonized by oak forest communities. From the southern end of the sand strip, close to the Pyrenees mountain range, to its northern end, there is a steep gradient of decreasing rainfall, providing an excellent space-for-time gradient to assess changes in oak seedlings-understory shrub interactions. Additionally, three oak species of contrasting functional strategies occur along the gradient: the temperate deciduous oak *Quercus robur* is present along the whole gradient, whereas two Mediterranean evergreen species occur at each end of the gradient, *Quercus ilex* in the dry north, and *Quercus suber* in the wet south.

These differences in forest composition provide an excellent natural context to also analyse the role of functional strategies in tree species responses to the effect of neighbours in contrasting climate conditions. Muhamed et al. (2013) analysed the associational patterns of the seedlings of those three oak species with understory shrubs at five positions along the climate gradient and both in closed forests and recent gaps. They found a switch from dominant negative associations in the wet southern end of the gradient to dominant positive associations in the dry northern end of the gradient and from closed forests to gaps. This result is highly consistent with facilitation theory predicting a switch from competition to facilitation with increasing stress (SGH hypothesis, Bertness and Callaway, 1994). Additionally, this result has important consequences for tree regeneration in a climate change-adapted management perspective. If drought strongly increases with climate change, as predicted for this region by modellers (IPCC, 2007), there should be a decrease in the competitive effect of understory species on tree seedlings in the wettest part of the gradient and thus less need to control forest weeds for regeneration success. Additionally, if facilitation increases at the driest end of the gradient, then foresters should rather conserve understory nurses to limit recruitment's mortality due to drought.

However, spatial associational patterns are not evidences of true interactions and the objective of this study was experimentally to test the hypothesis that interactions between oak seedlings turn from negative to positive with increasing drought stress along the climate gradient and with increasing light levels from forests to gaps. Additionally, we measured Vapor Pressure Deficit (VPD) in all treatment conditions in order to search for the driving mechanisms of oak seedlings-understory shrub interactions. Finally, Muhamed et al. (2013) could not adequately test the role of species strategies in their survey of associational patterns since the three oak species do not naturally occur all along the climate gradient. Thus, in this study we transplanted the three species at the two ends of the gradient to test also the role of functional tree strategies in their response to neighbours in a changing climate. We aim to answer to two main questions (i) Does the net effect of understory shrubs on early oak survival shift from negative to positive with increasing drought stress from the wet southern site to the dry northern one and from closed forests to gaps? (ii) Are oak species responses species-specific?

2. Materials and methods

2.1. Study sites and target species

The field experiment was conducted in the coastal forest sand dune communities of the Aquitaine region (south-western France). In Aquitaine, coastal dunes occur within an approximately 240 km-long sand strip stretching from the Gironde estuary in the north to the mouth of the Adour river in the south at the vicinity of the Pyrenees mountain range. The oak forest communities are located in inland fossile dunes, at approximately 1–10 km distances from the ocean. The soil is homogeneous all along the coast and is a young podzosoil with a pure coarse sand texture (Forey et al., 2008). The climate is overall temperate oceanic with the rainiest period during winter. However, there is a south–north gradient of decreasing mean annual rainfall with increasing distance from the Pyrenees mountain range, with a mean annual rainfall of 1300 mm in the south and 750 mm in the north. Mean annual temperatures also decrease slightly but significantly along this latitudinal gradient, from 14.1 °C in the south to 12.8 °C in the north (Sardin, 2009). Our experiment was conducted in two experimental sites located at both ends of this gradient because of their contrasting climate conditions, a wet southern site in Seignosse (43°41′N, 1°25′W) and a dry northern site in Soulac (45°32′N, 1°05′W). In 2011 the year where most of the measurements were carried out, annual precipitations, summer precipitations, annual temperatures and maximum summer temperatures were 1040 mm, 152 mm, 14.2 °C and 24.1 °C in the northern site, and 1473 mm, 215 mm, 15.75 °C and 25.9 °C in the southern site, respectively (Meteo-France data, 2011).

Three oak species dominate the forest communities, one deciduous species, *Q. robur*, and two evergreen *Q. suber* and *Q. ilex*. *Q. robur* is a common oak species in Europe, in particular in its northern and central parts where climate is temperate with no summer drought, whereas the two evergreen species are mostly found in the Mediterranean climate area of Mediterranean Europe and north-Africa. These two Mediterranean oaks may also occur within the warm temperate or submediterranean parts of Mediterranean Europe like is the case in the coastal dunes of the Aquitaine region. Thus, there is a strong difference in drought-tolerance between in one hand the deciduous temperate *Q. robur*, and the two evergreen Mediterranenan species (Tyree and Cochard, 1996). However, there are also differences in drought- and cold-tolerance between *Q. suber* and *Q. ilex* (David et al., 2007), the former inhabiting warmer and wetter Mediterranean climates than the latter (Michalet, 1991). In the coastal dunes of the Aquitaine region *Q. suber* is indeed mostly present in the south where the climate is wetter and milder, whereas *Q. ilex* is very abundant in the north where the climate is drier and less mild. However, these differences in geographical distribution may also be influenced by anthropogenic factors since both species are traditionally planted for ornamental reasons and *Q. suber* for cork production.

2.2. Experimental design

In early October 2010, we set up a split–split plot design with four factors: (i) site (Seignosse in the south and Soulac in the north, see above), (ii) canopy (forest and gap), (iii) neighbour (beneath shrub and shrub removed-plot hereafter will be denoted as with shrub and without shrub, respectively) and (iv) species (*Q. robur, Q. ilex,* and *Q. suber* seedlings). Within each site, we selected always in an east exposure, six forest plots and six gap plots for the canopy treatment, with a minimum of 500 m and maximum of 1500 m distance between plots. The size of each plot was approximately 100 ∗ 75 m. The forest plots were mature oak forests with at least 75% cover of adult oak trees and the gap plots were recent gaps (3–5 years), with no or very few remaining adult tree individuals in the overstory. For the neighbour treatment, which was embedded in the canopy treatment, we randomly selected, within each of the 12 plots from each site, 10 shrub individuals with approximately 10 m distance between them. The shrub species were the same in the gap and forest plots of each site but different across sites, with *Q. ilex* and *Q. robur* in Soulac (north) and *Q. suber* and *Ilex aquifolium* in Seignosse (south). The height and two crown perpendicular diameters of all shrub individuals were measured with a tape; height of the shrubs varied between 120 and 250 cm and their crown diameters between 140 and 240 cm, with no significant differences between sites and between gap and forest plots. The aboveground canopy of half of the shrub individuals from each plot was removed by severing stems at ground level and all regrowing stems were cut again at each seasonal survey when necessary.

For the species treatment, which was embedded in the neighbour treatment, we used 1–2 year-old bare-rooted oak seedlings of the three species that were collected in natural stands and transplanted in all experimental conditions. *Q. ilex* seedlings were collected at the northern site (Soulac), *Q. suber* seedlings at the southern site (Seignosse) and *Q. robur* seedlings at intermediate latitude (44.4°N, 1.16°W). Seedlings were carefully lifted out from the sandy soils, stored in moist sandy soil in plastic boxes, and then planted at each site within 2 days. Target seedlings were always planted in 20 × 20 × 20 cm manually dug holes located at the northern side of the shrub. The seedlings of the three target species were planted side by side, with at least 20 cm distance between them, both with and without shrubs. Thus, there were five seedlings per species, neighbour, canopy, and subsite and there were six subsites ($n = 240$ seedlings of each species). Hence, a total of 720 seedlings were planted in the whole design. In order to decrease the influence of transplantation shock, we replaced all dead seedlings (8.3% in Soulac and 11% in Seignosse), one month after planting, early November 2010.

2.3. Measurements

Survival and growth of each seedling was recorded 5 times during the experiment, early October 2010 immediately after planting, March 2011 after the first winter, June 2011 after the first spring, October 2011 after the summer and March 2012 after the second winter. Survival was calculated at each date per plot as a percentage of the five individuals transplanted per combination of the site × canopy × neighbour × species treatments. Survival was calculated at each date in a cumulative and non-cumulative way, in order to assess the outcome for the transplanted seedlings and to compare results among seasons, respectively. However, only final survival rates calculated following the former method are presented here. For growth we measured seedling height, stem diameter at collar height and number of green leaves, and calculated a relative growth increment during the whole experiment for each growth measurement ((final measurement/Initial measurement)/initial measurement). However, because of a too high mortality occurring in some treatments, we did not analyse growth data.

We used the Relative Interaction Intensity (RII) index to assess the effect of the shrubs on the oak seedlings (Armas et al., 2004). The RII index compares the performance of targets with and without neighbours as follows:

$$\mathrm{RII}_{shrub} = (S_{+N} - S_{-N})/(S_{+N} + S_{-N}) \tag{1}$$

where S is the mean of survival values of seedlings in the presence of shrubs ($+N$) and absence of shrubs ($-N$).

RII values are symmetrical around zero, varying between −1 and 1, with negative values for competition and positive values for facilitation. RII equal 0 when the net balance of interactions is neutral.

To assess the level of atmospheric stress occurring at each site × canopy × neighbour treatment combination condition, Vapor Pressure Deficit (VPD) was quantified by measuring air temperature and relative humidity at a height of 50 cm above ground level, using HOBO-Pro RH/Temp Data Loggers (Onset Computer Corp., Pocasset, MA, USA). We used three HOBOs per site × canopy × neighbour treatment combination. Temperature and relative humidity were registered each hour and the mean value of the maximum VPD per day was calculated for the April–August 2011 period. VPD was calculated as:

$$\mathrm{VPD}\ (Pascal) = ((100 - \mathrm{RH})/100)\ *\ \mathrm{SVP} \tag{2}$$

$$\text{where}\quad \mathrm{SVP}\ (Pascal) = 610.7 \times 10^{7.5T/(237.3+T)} \tag{3}$$

SVP and RH represent saturated vapor pressure and relative humidity.

2.4. Statistical analysis

Differences in oak survival rates due to the site, canopy, neighbour and species treatments were analysed with a split–split-plot ANOVA model, with site and canopy as main effects, neighbour as subplot effect and species as sub-subplot effect. Differences in RII values due to the site, canopy and species treatments were analysed with a split-plot ANOVA model, with site and canopy as main effects and species as subplot effect. Differences in VPD values due to the site, canopy and neighbour treatments were analysed with a split-plot ANOVA model, with site and canopy as main effects and neighbour as subplot effect. The effects of VPD (covariate) and of shrubs (factor) on final oak survival rates were analysed using an analysis of covariance (ANOVA model). Data were checked for normality and homogeneity of variance and all variables were log or arcsine-square root transformed before analyses to meet assumptions of parametric tests when necessary. Duncan multiple range tests were used to determine the significant differences between group's means when significant effects ANOVA occurred at $P < 0.05$. One-sample t-tests were also performed to test significant deviations of RII values from zero. All statistical analyses were carried out in SAS 9.2 (SAS Institute Inc., USA).

3. Results

The three oak species had strong and highly significant differences in survival at the end of the experiment (Table 1, and Fig. 1), with the highest survival for *Q. robur* (45.8 ± 4.2%), the lowest for *Q. suber* (16.6 ± 3.2%) and an intermediate survival for *Q. ilex* (25 ± 3.6%) (Duncan tests: a, c and b, respectively). When expressed in a non-cumulative way the strongest decline in survival

Table 1
Results of the four-way ANOVA for the effects of species, site, canopy, neighbours and their interactions on survival rates of oak transplants. Significant effects at $P < 0.05$ are indicated in bold.

Source of variation	*df*	Anova SS	Mean square	*F* value	Pr > *F*
Block	5	0.774	0.155	1.82	0.11
Site	1	0.385	0.385	4.53	**0.03**
Canopy	1	2.462	2.462	28.94	**<.0001**
Neighbour	1	0.409	0.409	4.8	**0.03**
Species	2	4.465	2.233	26.24	**<0001**
Site × canopy	1	0.343	0.343	4.03	**0.04**
Site × neighbour	1	0.741	0.741	8.71	**0.003**
Site × species	2	1.130	0.565	6.64	**0.001**
Canopy × neighbour	1	2.720	2.720	31.97	**<.0001**
Canopy × species	2	0.232	0.116	1.36	0.25
Neighbour × species	2	0.477	0.239	2.81	**0.04**
Site × canopy × neighbour	1	0.131	0.131	1.54	0.21
Site × neighbour × species	2	0.168	0.084	0.98	0.37
Site × canopy × species	2	0.416	0.208	2.45	0.09
Canopy × neighbour × species	2	0.230	0.115	1.35	0.26
Site × canopy × neighbour × species	2	0.411	0.205	2.41	0.07

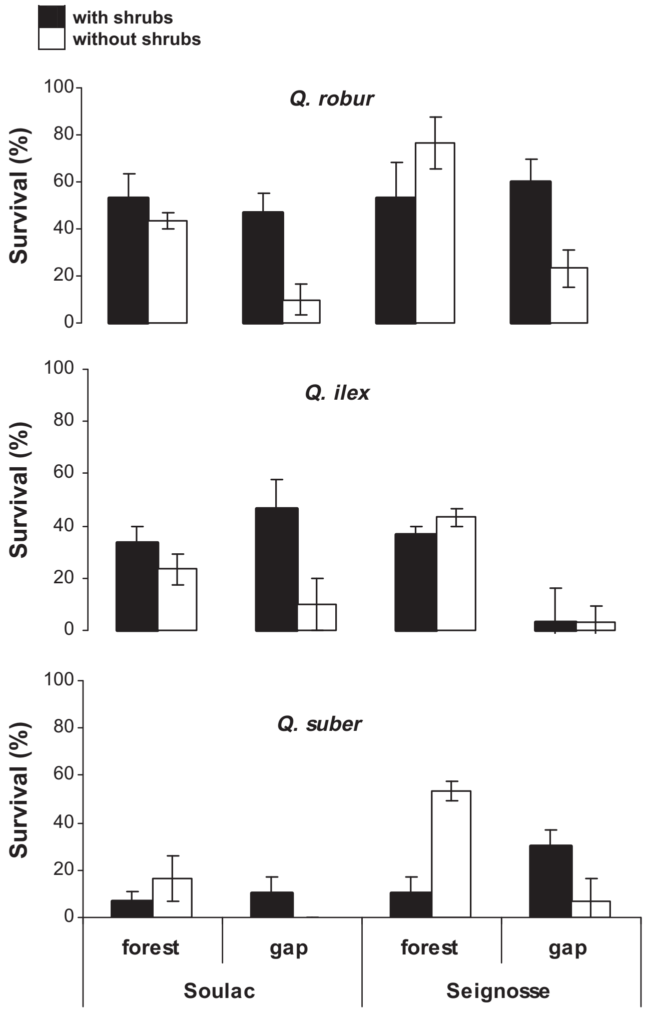

Fig. 1. Mean ($N = 6$) survival rates of the seedlings of the three oak species in the forest and gap plots of the dry northern site of Soulac and of the wet southern site of Seignosse. Shaded bars represent seedlings transplanted with shrubs and empty bars seedlings without shrubs.

occurred for the three species during the dry summer period (data not shown). There was also a highly significant canopy effect with a 45% higher overall survival in the forest plots than in the gaps (Table 1, and Fig. 1). The neighbour effect was weakly significant but there was a highly significant canopy × neighbour interaction, because shrubs increased survival 4 times in the gaps but decreased it by 1.3 times in the forests (Table 1, Fig. 1). There was also a weakly significant higher survival in the wet southern site of Seignosse than in the dry northern site of Soulac (33 ± 2.9% and 25 ± 3.6%, respectively). However, there were significant site × neighbour and site × species interactions, since shrubs ameliorated survival in Soulac but not in Seignosse and only *Q. robur* and *Q. suber* (but not *Q. ilex*) had a higher survival in Seignosse than in Soulac. Finally, there were only weakly significant site × canopy and neighbour × species interactions, due to a higher survival in forest plots than in gaps in Seignosse only and to a slightly overall positive effect of shrubs for the survival of *Q. robur* and *Q. ilex* but not of *Q. suber*, respectively (Table 1, Fig. 1).

There was a highly significant canopy effect on the RII index, because the shrubs strongly facilitated oak survival in the gap plots (RII = 0.48 ± 0.1) but reduced it in the forest plots (RII = −0.18 ± 0.1). There was also a significant site effect since the effect of shrubs was overall positive (RII = 0.34 ± 0.1) in the dry northern dunes from Soulac but null (RII = −0.04 ± 0.1) in the wet southern dunes from Seignosse (Table 2, Fig. 2). Although there were no significant interactions between the species and either the site or canopy treatments, results of sample *t*-tests show that only *Q. robur* and *Q. ilex* were significantly facilitated in the gap plots of Soulac and only *Q. robur* and *Q. suber* suffered from competition in the forest plots of Seignosse (Fig. 2).

VPD (kPa) was highly significantly affected by the canopy conditions, increasing from forest plots (1.10 ± 0.04) to gap plots (1.53 ± 0.05) (Table 3). VPD values were also higher without shrubs (1.40 ± 0.08) than with shrubs (1.23 ± 0.07) and in the dry northern dunes from Soulac (1.39 ± 0.07) than in the wet southern dunes from Seignosse (1.24 ± 0.08) (neighbour and site effects, respec-

Table 2
Results of the three-way ANOVA for the effects of site, canopy, neighbours and their interactions on the Relative Interaction Intensity (RII) index for the survival of oak transplants. Significant effects at $P < 0.05$ are indicated in bold.

Source of variation	*df*	Anova SS	Mean square	*F* value	Pr > *F*
Block	5	0.791	0.158	0.54	0.74
Site	1	2.577	2.577	8.74	**0.004**
Canopy	1	7.869	7.869	26.69	**<.0001**
Species	2	1.208	0.604	2.05	0.13
Site × canopy	1	0.010	0.010	0.03	0.85
Site × species	2	0.880	0.440	1.49	0.23
Canopy × species	2	0.681	0.340	1.15	0.32
Species × site × canopy	2	0.829	0.415	1.41	0.25

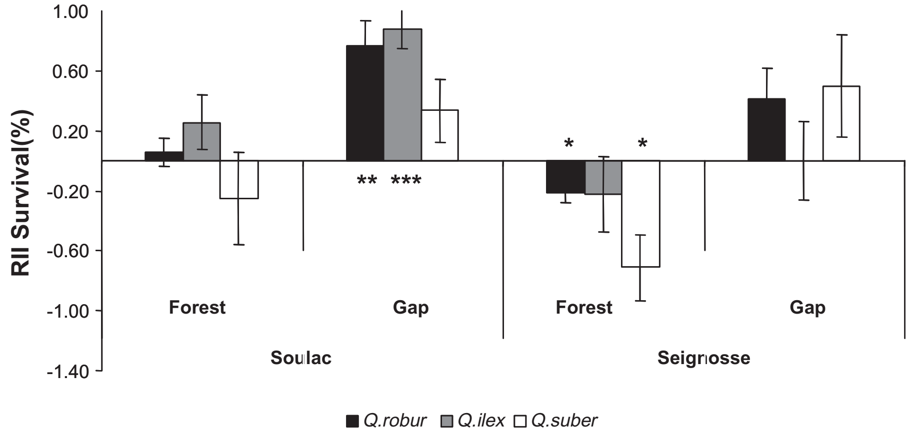

Fig. 2. Mean ($N = 6$) Relative Interaction Intensity (RII) index calculated for the survival of the three oak species transplanted in the forest and gap plots of the dry northern site of Soulac and of the wet southern site of Seignosse. Asterisks indicate significant deviations of RII values from 0 (one-sample t test): $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 3
Results of the three-way ANOVA for the effects of site, canopy, neighbours and their interactions on mean values of VPD measured from April to August 2011. Significant effects at $P < 0.05$ are indicated in bold.

Source of variation	*df*	Anova SS	Mean square	*F* value	Pr > *F*
Block	2	0.002	0.001	0.11	0.89
Site	1	0.145	0.145	12.02	**0.003**
Canopy	1	1.092	1.092	89.97	**<.0001**
Site × canopy	1	0.001	0.001	0.15	0.70
Neighbour	1	0.179	0.179	14.78	**0.001**
Sit × neighbour	1	0.007	0.007	0.65	0.43
Canopy × neighbour	1	0.012	0.012	1.02	0.33
Site × canopy × neighbour	1	0.015	0.015	1.27	0.27

tively, Table 3). There were no significant interactions among any of the three factors (Table 3). Interestingly, variation in VPD values strongly explained differences in survival among oak seedlings from without shrubs plots, but not among seedlings from with shrubs plots ($F_{\mathrm{VPD}\times\mathrm{neighbours}} = 6.4$, $df = 1$, $P = 0.02$, Fig. 3). This suggests that shrubs facilitated oak seedlings from highly stressed conditions by reducing VPD values.

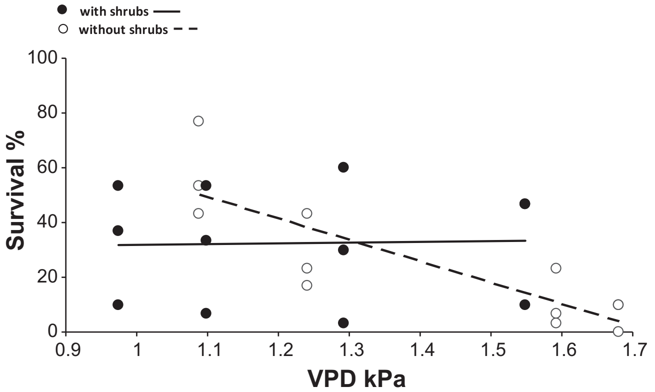

Fig. 3. Oak seedlings survival (%) as a function of the average Vapor Pressure Deficit (VPD) measured with shrubs (solid circle) and without shrubs (open circle). The solid line represents the non significant regression line of the with shrubs plots and the dashed line the regression line of the without shrubs plots. VPD values represent the mean value of the maximum daily VPD from April to August 2011 period.

4. Discussion

Our results provide evidences of significant effects of understory shrubs on oak seedling survival in the coastal sand dune forests of the south-western of France. These effects strongly vary among sites and canopy conditions, with a shift from negative to positive interactions with increasing drought along the climate gradient and from closed forests to gaps. In addition, our VPD measurements showed that the process involved in the positive effect of the shrubs in dry conditions was certainly a decrease in atmospheric water stress below their canopies. In contrast, differences in species responses to the effects of understory shrubs were weak and not clearly related to species ecological requirements and geographical distributions. Interestingly, our results were very consistent with the spatial study of associational patterns of oak seedlings of Muhamed et al. (2013). Thus, although short, our experiment provides robust results highlighting the major plant-plant interactions occurring in this system and allowing us to draw realistic recommendations for managing oak regeneration in a climate change-adapted forest management perspective.

4.1. Variation in oak seedlings responses to understory shrubs with site and canopy conditions

The most significant result of our study was the shift in interactions occurring between understory shrubs and oak seedlings due to the combined effects of canopy and climate conditions (site effect). The effect of the shrubs on oak seedlings survival strongly shifted from a negative net balance in the forest plots of the wet southern site to a positive net balance in the gap plots of the dry northern site, with no significant interactions in intermediate conditions (i.e., gap plots of the south and forest plots of the north). This result strongly supports the Stress Gradient Hypothesis (Bertness and Callaway, 1994; Callaway, 1997; Holmgren et al., 1997) proposing that the net effect of neighbours should turn from negative to positive with increasing environmental stress. This is also consistent with the results of a number of experiments conducted along spatial or temporal water stress gradients (Callaway et al., 1996; Greenlee and Callaway, 1996; Gómez-Aparicio et al., 2004; Sthultz et al., 2007; Cuesta et al., 2010).

However, other studies have found conversely an increase in competition with increasing water stress (Tielborger and Kadmon, 2000; Maestre and Cortina, 2004), which induced an important debate on variation in plant interactions along water stress gradient (Maestre et al., 2005; Lortie and Callaway, 2006). It has been suggested that these discrepancies may be due to different stress factors involved along complex aridity gradients, with an increase in water resource stress more likely inducing an increase in competition and an increase in atmospheric water stress more likely inducing an increase in facilitation (Michalet, 2007; Gómez-Aparicio, 2009; Maestre et al., 2009). In our study we did not detect significant negative effects of shrubs at the dry end of the gradient suggesting that the shrub-seedlings interactions were more likely driven by atmospheric moisture stress (non-resources stressor) rather than below-ground soil water stress (resources stressor). This hypothesis was proposed by Michalet (2007) and supported by the study of Saccone et al. (2009) who found, for different tree species depending on their functional strategies, either an increase in facilitation with increasing Vapor Pressure Deficit (VPD) or an increase in competition with increasing soil water stress. Our measurements of VPD strongly suggest that the positive effects of understory shrubs on oak seedlings in the gap plots of the dry northern site was due to reduced atmospheric stress below their canopy. Indeed, we found a significant negative correlation between VPD values and oak survival for seedlings planted without shrubs but not for seedlings planted below shrubs. Thus, our study provides additional evidence that facilitation should increase with increasing water stress when the stress for the target species is rather atmospheric than resource-based (Valiente-banuet and Ezcurra, 1991; Gómez-Aparicio et al., 2005; Saccone et al., 2009; Cuesta et al., 2010).

4.2. Species-specificity of oak seedlings responses to treatments

We observed strong and significant survival differences among target species, with a much higher survival for the deciduous oak, *Q. robur*, than for the two evergreen Mediterranean oaks. Additionally, *Q. robur* and *Q. suber* had a higher survival in the wetter and milder climate of the south, whereas there were no differences among sites for *Q. ilex*. The stronger overall survival of *Q. robur* may be explained by its deciduous habit and pioneer strategy and thus a likeable lower sensitivity to transplantation shock (Rameau et al., 1993; Rozas, 2003; Cater and Batic, 2006). The lower sensitivity of *Q. ilex* to site conditions, and in particular its higher survival in the stressed northern site as compared to the two other species in Seignosse, is consistent with its higher tolerance to physical stress and natural dominance in the north. Indeed, ecophysiological comparisons of the two Mediterranean species have shown that *Q. ilex* is more drought-tolerant than *Q. suber* (David et al., 2007). Additionally, the two species have contrasted climate distributions within the Mediterranean region, the former inhabiting colder and drier climates, both in Europe and north-Africa than the latter (Ozenda, 1985; Michalet, 1991). This is consistent with the *high* mortality rate of *Q. suber* in the dry northern dunes of Soulac.

Although the three target oak species have contrasted ecological requirements, as suggested by their different climate distribution throughout Mediterranean Europe and north-Africa, they had surprisingly very weak differences in responses to the effects of both the understory shrubs and canopy conditions. We only observed a weakly significant species × neighbour interaction in the four way ANOVA model on survival data, due to a slightly overall positive effect of shrubs for the survival of *Q. robur* and *Q. ilex* but not of *Q. suber*. However, there was no significant species effect in the three-way ANOVA model on RII values. This weak species-specificity of oak seedlings in responses to the effects of neighbours is quite surprising since most biotic interactions studies have highlighted that species functional strategies highly contribute to explain variation in species interactions along environmental gradients (Gómez-Aparicio et al., 2004, 2009; Liancourt et al., 2005; Saccone et al., 2009, 2010; Forey et al., 2010). Drought-tolerant species have been shown to be very sensitive to competition, whereas shade-tolerant species are in opposition very sensitive to facilitation (Michalet et al., 2006). In our study differences in species responses were weak and rather unclear since, for example for the two Mediterranean species, the least stress-tolerant oak, *Q. suber*, showed a tendency to be less facilitated than the most stress-tolerant one, *Q. ilex*. This low species-specificity observed in our experiment may be due to either low difference in shade tolerance among the three target oak species and/or to overwhelming effects of site and canopy conditions or a too small number of seedlings.

4.3. Implications for oak regeneration in a climate change-adapted management perspective

Our experiment provides clear evidence that (i) macro- and microclimate conditions due to site and canopy conditions, respectively, strongly determine the direction and strength of interactions of oak seedlings with understory shrubs, and (ii) oak seedling functional strategies had conversely no influence on understory shrubs-seedlings interactions strength. This result is highly consistent with the spatial patterns of associations of natural recruits of the same species with understory shrubs surveyed by Muhamed et al. (2013) in the same system but including a more important number of forest and gap plots. They found a clear shift from negative associations of oak seedlings with understory shrubs in the forest plots of southern wet sites to positive associations in the gap plots of northern dry sites, with neutral associations in intermediate geographical and canopy per site conditions. Additionally, they also found no effects of oak species functional strategies on associational patterns. This suggests that, although short our experiment provides robust evidences of the dominant interactions occurring between understory shrubs and natural oak recruits in this system. In other words, the results of our experiment were not just representative of the particular climate conditions that stochastically occurred the years of our study.

This certainly allows us to propose realistic recommendations for managing natural oak regeneration in a climate change-adapted forest management perspective. Current knowledge issued from climate models predicts an increase in temperature and summer aridity for the Aquitaine region, as is the case for other parts of Mediterranean Europe (IPCC, 2007). Following the results of our experiment and the survey of associational patterns of Muhamed et al. (2013) on a spatial gradient of increasing water stress, and consistent with facilitation theory (Bertness and Callaway, 1994; Brooker, 2006; McIntire and Fajardo, 2009), we may predict that increasing water stress with climate change should induce a decrease in the negative influence of understory shrubs in the most benign physical conditions (closed forest plots from the south) and an increase in their positive effects in the most severe environmental conditions (gaps from the north). Thus, it is reasonable to consider that forest managers may in the future reduce forest weed control in the south of Aquitaine due to decrease competition with oak recruits and rather conserve understory shrubs and/or tree shelter in the north to maintain a sufficient oak recruits survival. In contrast, although longer experiments with a higher replication effort may reveal more clear results on the effects of oak species functional strategy, our study does not provide evidence that foresters should adapt their management of understory shrubs to particular oak species in this system.

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Appendix A

Mean survival rates of the seedlings of pooled oak species with and without shrubs in the forest and gap plots (Fig. 1), in the dry northern site of Soulac and the wet southern site of Seignosse (Fig. 2), and the survival rates of the seedlings in both sites under different canopy conditions (Fig. 3). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Fig (1)

Fig (2)

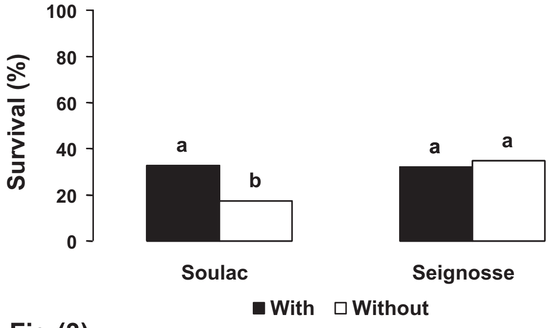
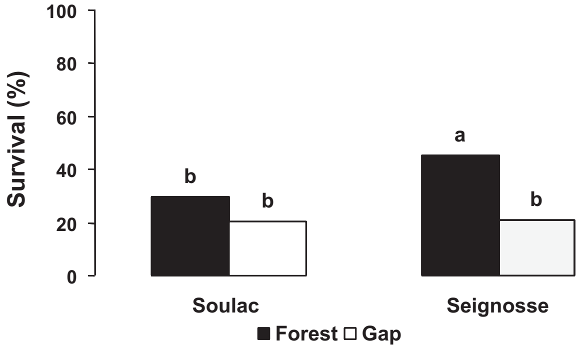


Fig (3)



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