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Can we use shelterwoods in Mediterranean pine forests to promote oak seedling development?

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Abstract

The use of shelterwoods to favour the development of natural or underplanted seedlings is common in temperate forests but rare in the pine forests of the Mediterranean area. Our aim was to assess the use of shelterwoods in Aleppo pine (*Pinus halepensis*) woodlands in southern France to promote the survival and growth of two co-occurring oak species: the deciduous *Quercus pubescens* and the evergreen *Quercus ilex*.

Twelve Aleppo pine stands were selected and differentially thinned to create a light shelterwood ($G = 32 \text{ m}^2/\text{ha}$, irradiance 13%), a medium shelterwood ($G = 19 \text{ m}^2/\text{ha}$, irradiance 33%) and a dense shelterwood ($G = 10 \text{ m}^2/\text{ha}$, irradiance 52%). A total of 1248 sowing points, half composed of *Q. pubescens* and half of *Q. ilex*, were then set up in these three conditions. Seedling survival and growth were monitored for three years and plant stress was assessed by measuring predawn leaf potential and photosynthetic performance through the F_v/F_m ratio. Soil moisture was also recorded at two depths during two growing seasons.

Survival was high for both species in all three conditions due to three consecutive wet years. The lowest survival was recorded for *Q. pubescens* in the dense shelterwoods. Growth in diameter and height increased from the dense to the light shelterwoods. Shrubs developed more strongly in the light shelterwood, and increasing shrub cover enhanced height growth. Photosynthetic performance was lowest for *Q. pubescens* in dense shelterwoods and highest in light shelterwoods, whereas the reverse was true for *Q. ilex*. The lowest predawn potentials were recorded in the dense shelterwoods even though higher soil water content values were measured in this treatment during the summer drought.

We show that light shelterwoods were more beneficial to growth than denser ones, indicating control by light availability during the three years of the study. However, as lower soil moisture and faster understorey development were also recorded in this condition, more extended observation is needed to determine whether this benefit persists in subsequent years.

Key words: Thinning, Seedling growth, Soil water content, *Pinus halepensis*, Winter deciduous oak, Evergreen oak

1. Introduction

Aleppo pine (*Pinus halepensis* Mill.) is one of the major pine species in the Mediterranean basin due to its high colonizing capacity and remarkable adaptation to the environmental constraints of the Mediterranean area. However, its spread has also been largely promoted by human action. For instance, in the Iberian Peninsula 43% of the *P. halepensis* forest results from afforestation (Vélez, 1986) and 80% of the plantations were initiated with this species in Israel (Ginsberg, 2006). In southern France, Aleppo pine has also largely developed in recent decades – its present cover is estimated at 250 000 ha – mainly by natural colonisation after the collapse of the traditional agricultural system in the 1950s.

Aleppo pine woodlands, either planted or naturally established, have long been considered as a favourable habitat to promote a natural transition towards vegetation dominated by broadleaved species. This assumption has mainly been supported by the intermediate successional status of Aleppo pine forests between shrub or herbaceous vegetations and late-successional hardwoods (Barbéro et al., 1998; Pausas et al. 2004). However, this supposed facilitating process is currently a subject of debate. In semi-arid Mediterranean areas, manipulative studies show a negative impact of *P. halepensis* cover on the late successional woody species (Maestre et al., 2003; Bellot et al., 2004). Similarly, Maestre and Cortina (2004) in a review study emphasize the negative consequences of Aleppo pine forests on spontaneous vegetation, water use and soil losses. By contrast, in more humid conditions, observational data suggest a positive influence of Aleppo pine on late-successional broadleaved species (Lookingbill and Zavala 2000; Zavala et al., 2000). In addition to climatic and other abiotic conditions, the structure of the pine overstorey in relation with understorey development also seems to play a role in the successful establishment of late-successional ligneous species. Assessing how pine plantations could successfully promote the recovery of the native vegetation along biotic and abiotic gradients in southern Spain, Gómez-Aparicio et al. (2009) showed the negative influence of dense, closed overstorey. By contrast, moderate densities were favourable to species recruitment, suggesting the existence of facilitative interactions.

Although the role of Aleppo pine stands on the successional ligneous vegetation is controversial, experience with Aleppo pine overstorey manipulations is particularly scant in the Mediterranean area. Typically, the shelterwood regeneration method is commonly used in temperate forests to favour the establishment and growth of late-successional tree species (e.g. Gemmel et al. 1996, Agestam et al. 2003), but has seldom been tested in the Mediterranean conifer forests (Rodríguez-Calcerrada et al., 2008). In the shelterwood treatment, the degree of openness of the overstorey is used to control light availability and so influence the growth of naturally established or underplanted broadleaf seedlings (Beaudet and Messier 1998, Coll et al., 2003). Changes in microclimatic conditions and in water regime are other direct consequences of the presence of shelterwoods (Madsen and Larsen 1997). Shelterwoods also control the development of the ground vegetation that can compete with tree seedlings for light, water and nutrients (Nambiar and Sands 1993, Davis et al. 1999) and can thus severely limit seedling development (Löf 2000).

Our objective was to assess how successfully shelterwoods could be used in Aleppo pine forests to promote survival and growth of introduced seedlings. For this purpose we designed an experiment in which Aleppo pine stands underwent different degrees of thinning. Treatments effects were then assessed by analysing the changes in abiotic and biotic environmental factors and the performance of oak seedlings established in the different conditions obtained. We hypothesized that (i) dense shelterwoods would produce the conditions most detrimental to seedling survival and growth, (ii) lower seedling performance in dense shelterwoods would be linked to lower light and soil water availability and (iii)

ground vegetation would benefit from pine canopy openness and thereby limit seedling growth.

2. Materials and methods

2.1 Study area

The experimental site was located in a protected natural area near the Étang de Berre, a coastal lagoon adjacent to the Mediterranean Sea west of the city of Marseille in southern France.

The landscape of this area is covered by Aleppo pine forests, shrublands (*garrigues*) and some residual agricultural areas. The mean annual temperature is 14.5 °C and the annual rainfall is 406 mm (computed over the period 1961–1996). We note that during the three years of the experiment, rainfall was largely higher than the mean, with respective values of 779, 697 and 662 mm in 2008, 2009 and 2010.

The experiment was set up on a flat area (mean altitude 130 m). This area had previously been used as cropland and divided up into small fields bounded by stone walls, the remains of which were still visible. The current vegetation was dominated by Aleppo pine, which had become naturally established after land abandonment, forming closed stands 40 to 50 years old that had not been affected by wildfires at least during the past four decades. The dominant layer was composed of Aleppo pine, the evergreen holm oak (*Quercus ilex* L.) was present in the subcanopy layer, the shrub layer was dominated by *Q. coccifera* L., *Q. ilex*, *Rosmarinus officinalis* L., *Phyllirea angustifolia* L. and the herb layer was scant. *Q. pubescens* Wild. (a deciduous co-occurring oak) did not form woodlands close to the study area and only individual trees could be found. At a broader regional scale, *Q. ilex* was found preferentially in drier site conditions and poorer soils, but *Q. pubescens* and *Q. ilex* had overlapping ranges and coexisted in many habitats. Owing to the long history of anthropogenic disturbances in this area, it was not clear from the current distributions of the two oak species what the relative contributions of environmental factors and human actions were.

The soils had developed on a calcarenite bedrock composed of sandy limestone material and fossil shells. Alteration of this bedrock had led to calcareous soils, composed of a first organic layer 5–10 cm thick and a second sandy loam layer 20–40 cm thick.

2.2 Thinning experiment and acorn sowing

We selected 12 abandoned fields with a dense cover of pine on which we set up twelve 25 m × 25 m plots (one plot/field). We then applied one of the three thinning treatments to each plot in October 2007: (i) heavy thinning removing 2/3 of the basal area, to give light shelterwood (Light Shelterwood LS), (ii) moderate thinning removing 1/3 of the basal area (Medium Shelterwood MS) and (iii) no thinning (Dense Shelterwood DS). Plots were inventoried before and after the thinning by recording girth at breast height of all trees >1.30 m and thinning was practised from below.

Acorns from *Q. ilex* and *Q. pubescens* were collected in November 2007 using different sites and several trees per site for each oak species. Sites were located near the experimental stand and in comparable ecological site conditions. Non-viable acorns were eliminated by the floating method and visual screening. Acorns were sown at sowing points of three acorns. The three acorns 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. The wire mesh had been previously left for 24 h in an acid solution to favour its corrosion.

The sowing points were arrayed in each plot in 8 rows of 13 points each. They were spaced 1 m apart from each other on the row, alternating *Q. ilex* and *Q. pubescens*. The distance between rows was 2 m. A total of 104 sowing points of three acorns per plot were installed (half *Q. ilex* and half *Q. pubescens*) in late November 2007, forming a grand total of 1248 sowing points for the whole experiment. During spring 2008 we observed signs of predation by rodents on *Q. pubescens* seedlings only and a protection net (height 40 cm, mesh size 0.8 cm) was accordingly placed around all the *Q. pubescens* sowing points.

2.3 Environmental factors: light, soil moisture and soil temperature

In July 2008, light measurements were made on clear days using five solarimeter tubes per plot (300–3000 nm, Delta-T Device), leaving two tubes in full light conditions. The light transmittance was then computed by averaging the below/above ratios per plot and per treatment. Light quality was measured in nine plots (three plots per treatment) using a spectrometer (Spectro-Vio C5210-C5220, Korea Materials & Analysis Corp. K-MAC). Measurements were taken at five locations per plot. The red-far red ratio (R:FR) was computed as the ratio of photon irradiance at 660 nm to the photon irradiance at 730 nm. Following Aphalo and Lehto (1997), transmission of light in the blue region was taken as the ratio of photon irradiance at 450 nm under the canopy to photon irradiance in full light conditions.

Soil water content (SWC) was measured at different time intervals during the 2009 and 2010 growing seasons using a TDR profile probe (PR2, Delta-T Devices) equipped with five electronic sensors arrayed at fixed intervals. The probe was inserted in an access tube driven into the soil, and we took the average of three readings at each location by rotating the probe through 120°. Nine plots distributed among the three thinning treatments were equipped with four access tubes per plot. Owing to soil stoniness, access tubes were installed at ranging depths. Thus for each tube the depth at which SWC was measured varied and soil water measurements were finally used for only the two soil depth classes 10–30 cm and 30–50 cm. Soil temperature was measured at three dates during summer 2009 by inserting a probe (Wet2, Delta-T Devices) in the upper soil layer (10 cm depth). At each date, six sampling points distributed along a transect were measured per plot, and three measurements were made per point.

2.4 Vegetation measurements

The emerged seedlings were counted in June 2008 and surviving seedlings were recorded and measured (height and stem base diameter) at the end of each year from 2008 to 2010. Some apparently dead seedlings, with no green leaves and brittle stems, were able to recover and resprout after the summer period, and were therefore counted as alive. The soil surface was characterized at the same time inside a 25 cm-radius hoop centred on the sowing point. Cover of bare soil, litter, grass species and shrub was estimated using an abundance dominance coefficient derived from the Braun-Blanquet method: 1 presence, 2 < 5%, 3 = [5–25%], 4 = [25–50%], 5 = [50–75%], 6 = [75–100%]. For subsequent computations, the midpoint of each class was used. Mean shrub height was measured during the last growing season using 15 points per plot distributed along five transects. Shrub cover was also visually estimated at plot scale.

2.5 Fluorescence and leaf water potentials

Measurements of fluorescence were made to estimate the photosynthetic performance of the plants in the different treatments. Measurements were made each month in 2009 from May to October in the morning (9:00–11:00). We used a portable fluorimeter (Pocket Pea, Hanstech Instruments) and leafclips to allow dark adaptation of the sampled leaf (minimum time 30 min). Ten *Q. pubescens* and ten *Q. ilex* seedlings were sampled in each plot (one measurement per seedling) and used for all the measurements. Maximal (F_m) and minimal (F_0) fluorescence were used to calculate maximum efficiency of the photosynthetic energy conversion of photosystem II ($F_v/F_m = [F_m - F_0]/F_m$).

To determine the water status of the seedlings during the summer period, predawn leaf water potential was measured on 16 July 2008 after a short period of dryness and on 15 September 2009 after a long period of dryness. A total of 16 seedlings per species and per treatment were sampled. Before sunrise (solar time 3:30–5:00), a leaf was cut from the oak seedling, placed in a plastic bag and transported in an icebox for immediate in-field measurement with a pressure chamber (PMS/1000, PMS Instrument).

2.6 Data analysis

Differences between treatments and species and the interaction between these two factors were analysed using two-way analyses of variance (ANOVA) followed by a Tukey *post hoc* test. Before ANOVAs, assumptions of normality and homoscedasticity were checked. Mathematical transformations of data were used when necessary to correct deviations from normality and heterogeneity of variances. When these conditions could not be met the non-parametric Kruskal-Wallis test was used (soil water content and seedling survival). For seedling survival, to detect which of the treatments differed significantly at a confidence level of 95%, we used the Nemenyi test (Nemenyi, 1963).

Statistical analyses were performed using Statgraphics Centurion XV (StatPoint Inc.) and R software (R development Core Team, 2005).

3. Results

3.1 Stand characteristics after thinning

The treatments deeply modified stand characteristics (Table 1). The heavy thinning (LS treatment) produced stands with an open tree layer cover providing a light transmittance of 52%. By contrast, light transmittance was reduced by about 20% in the MS treatment and by 40% in the unthinned stands (DS treatment) with respective light transmittance values of 33% and 13%. Light quality was also modified, as we noted decreasing R:FR and blue light ratios from the light to the dense shelterwoods.

In relation to these contrasting light availability values, the stands in the LS treatment exhibited a more developed shrub cover than those of the MS treatment, whereas shrub cover was sparse in the stands of the DS treatment. Shrub cover was mainly composed of *Q. coccifera*, which represented 47%, 61% and 77% of the total shrub cover in the LS, MS and DS treatments respectively, and secondarily by *Q. ilex*. Mean shrub height significantly increased from LS to DS. Litter cover, mainly pine needles, was highest in the DS treatment and lowest in the LS treatment, although differences were not significant. Herbaceous cover was nil in the stands before thinning and negligible three years after thinning.

3.2 Soil water content and soil temperature

Soil water content (SWC) followed the same general pattern during the growing season for the two years and the different treatments (Fig. 2). SWC peaked in spring and then decreased sharply with the drop in rainfall in late spring, reaching a minimum in late summer. It then rose again with the return of autumnal rain. However, SWC values in autumn remained lower than those recording in spring even after heavy rainfall such as in September 2009 (113 mm in two days). In the upper soil layer, SWC was lower in the DS treatment than in the other two treatments in spring and early summer, whereas in summer SWC tended to be lowest in the LS treatment and highest in the MS treatment, although differences were not significant. In the deeper soil layer, trends were more marked between the treatments in the summer period: SWC was lowest in the LS treatment and highest in the DS treatment, SWC in the MS treatment being close to the values of the DS treatment.

Soil temperature (Fig. 3) during the summer period was appreciably higher under the opened pine cover of the LS treatment than in the other two treatments. We found no differences between DS and MS during that period.

3.3 Oak seedling survival and growth

Three years after treatment application, seedling survival was higher for *Q. ilex* than for *Q. pubescens* in the DS (Kruskall-Wallis test, $P < 0.001$) and MS treatments ($P < 0.001$), but not in the LS treatment ($P = 0.82$). As shown in Fig.1, *Q. pubescens* survival was appreciably lower under the dense shelterwood than under the two other shelterwood types. By contrast, differences in survival among the treatments were less marked for *Q. ilex*, although survival was higher in the medium shelterwood treatment at all dates. We did not find any effect of shrub cover on survival (data not shown), although growth was affected (see below).

Stem diameter and height significantly increased from the DS treatment to the LS treatment for both species (Fig. 4), and *Q. pubescens* growth was lower than *Q. ilex* growth in all three treatments. By contrast, the height-diameter ratio decreased from the DS to LS treatments, the *Q. ilex* seedlings being more slender (tall and thin) than the *Q. pubescens* seedlings in MS and LS ($F = 22.02$, $P < 0.001$ and $F = 29.45$, $P < 0.001$).

Concerning the influence of shrub cover on seedlings dimensions in the MS and LS treatments, we did not find any effect on stem diameter ($P=0.60$ and $P=0.16$ for *Q. pubescens* and $P=0.39$ and $P=0.23$ for *Q. ilex*). However, shrub cover influenced height in both species (Fig 5), seedlings being taller with increasing shrub cover. This effect was more marked in the LS treatment, where shrubs were more abundant.

3.4 Fluorescence and leaf water potential

Maximal photochemical efficiency of PSII (F_v/F_m) showed a decrease for both species during the summer period (Fig. 6). Nevertheless, the responses of the two oak species were remarkably different according to the treatment. For *Q. pubescens*, lowest values were recorded in the DS treatment, and similar values were recorded in the MS and LS treatments. Conversely, for *Q. ilex*, highest values were found in the DS treatment, and lowest values in the LS treatment, values in the MS treatment lying between these extremes.

Predawn leaf water potentials were lower in *Q. pubescens* than in *Q. ilex* for the two dates, but the difference was significant only in September 2009, when the seedlings experienced a major drought stress ($\psi_{pd} = -5.09$ Mpa for *Q. pubescens* and $\psi_{pd} = -4.16$ Mpa for *Q. ilex* in all treatments, $P < 0.001$). The lowest potentials were recorded in the DS treatments for both species and both dates (Fig. 7). Potentials in the MS treatment were significantly lower than those in the LS treatment in July 2008 only.

4. Discussion

4.1 Light and soil water availability

Not surprisingly, light availability was correlated with degree of thinning. This resource was primarily controlled by the upper pine cover, as the shrub layer was weakly developed at the beginning of the experiment and the shelterwood treatments had generated a light resource gradient. Along with light availability, light quality was modified, an alteration also noted by Gasque and Garcia-Fayos (2004) under Aleppo pine cover.

Unexpectedly, soil water content was similar or slightly lower in the dense shelterwoods than in the two other shelterwood types in the upper layer only and before the summer period. By contrast, in the deeper layer, SWC was significantly higher during the summer period in the dense shelterwoods. This result is at variance with the finding of Bellot et al. (2004) who observed a negative effect of Aleppo pine on soil moisture in SE Spain, particularly in the 0–10 cm layer, an effect that increased with tree density. However, Maestre et al. (2003) did not report any such negative effect in the 0–20cm soil layer between microsites located under Aleppo pine canopy and open areas without vegetation. Koehlin et al. (1986) also found a negligible effect of Aleppo pine on the soil water balance in the 0–15 cm soil layer in southern France.

In this experiment, unlike the above studies, deeper layers were measured and, which showed that SWC in the upper layers did not necessarily reflect SWC of in the deeper layers. The moderate reduction of SWC in the 10–30 cm layer recorded before the drought period in the dense shelterwoods can be explained by rainfall interception by the closed pine canopy. However, during the drought period, the more pronounced decrease in soil moisture recorded in the light shelterwood treatment could be the result of: (i) a greater soil evaporation due to a higher temperature, as recorded in this study, (ii) a greater transpiration from the more abundant understorey and, (iii) a limited transpiration of the upper pine canopy due to stomatal closure, as Aleppo pine has been shown to reduce its

transpiration sharply during drought periods (Schiller and Cohen, 1998). In a study comparing a thinned *vs.* an unthinned *P. ponderosa* stand in Arizona, Simonin et al. (2007) showed that the importance of the understory evapotranspiration was greater in thinned than in unthinned plots, and increased during extreme drought, when overstory transpiration was low. Similarly, Kurpius et al. (2003) found that soil evaporation accounted for about 50% of the total stand evaporation during summer and autumn in a *P. ponderosa* plantation in California. In a semi-arid Aleppo pine stand of in southern Israel, Raz-Yaseef et al (2010) reported soil evaporation fluxes in sun-exposed areas double those in shaded areas, and higher soil water content in the latter areas than in the former areas during the drying season. Differences in soil moisture between the light shelterwood treatment and the other treatments were greater in the deeper layer. This result might be due to preferential water uptake by the understorey at this depth, but further investigations is needed to confirm this hypothesis.

4.2 Oak seedling survival and growth

Oak survival after 3 years was shown to vary markedly for *Q. pubescens* only, survival being appreciably reduced under the dense shelterwood. This result is in line with the lower tolerance to shade of *Q. pubescens* compared with *Q. ilex* and with the higher physiological stress undergone by the seedlings of this species in such conditions (see below). In previous experiments conducted under a light pine cover in the same area and with the same species (Prévosto et al., 2011), we reported a much lower survival rate of the seedlings one year after emergence, and *Q. pubescens* was more strongly affected than *Q. ilex* (survival of 16% and 53%, respectively). However, unlike the earlier study, the present experiment benefited from three consecutive ‘wet’ years, which explains, in part, this much higher survival. Regeneration dynamics of Mediterranean species have been shown to depend strongly on the recruitment peaks that occur in sporadic ‘wet’ years (Gómez-Aparicio et al., 2005, 2008).

Supporting our initial assumption, growth in height and diameter for both species was enhanced by canopy openness, related to higher light availability. In the most shaded conditions of the dense shelterwoods, reduced light was the main factor limiting growth, although soil water content was comparable (in the upper soil layer) or even higher (in deeper soil layers) during the summer drought period. The observed pattern of growth increase with light is consistent with previous studies in the Mediterranean area (e.g. Sánchez-Gómez et al., 2006; Pérez-Ramos et al., 2010), although others found that intermediate light conditions were the most growth-enabling (e.g. Puerta-Piñero et al., 2007; Quero et al., 2008). These results also confirm the predominant successional status of *Q. ilex* after pine colonisation in this area, *Q. ilex* outperforming *Q. pubescens* in both survival and growth under all three stand conditions.

In shade conditions, seedlings of both species were slender (tall and thin) compared with seedlings growing in stronger light conditions, as shown by the decreasing values of the height-diameter ratio from dense to light shelterwoods. In the dense shelterwoods light is less abundant and its spectral quality is changed, with reduced values of red-far red and blue light ratios. These modifications lead to stimulation of plant elongation typical of shade avoidance (Franklin, 2008).

The influence of shrubs in oak tree species establishment has been seldom studied under afforested conditions. Here, shrubs had no effect on the survival of oak seedlings, whereas clear facilitative effects are usually found in open conditions due to reduction of water stress and direct radiation (Castro et al., 2004; Gómez-Aparicio et al., 2006; Smit et al., 2008). The role of the shrub layer in attenuating the extreme climatic conditions prevailing in open areas (e.g. high radiation, high or low temperatures) were probably weaker here, as this role was played primarily by the pine canopy. Shrub cover only enhanced height elongation, and this

effect was more pronounced under the light shelterwoods. Shrubs, by physically preventing lateral expansion of the seedlings and by modifying light availability and quality, enhanced stem elongation, but left growth in diameter unchanged. We note that shrubs may also limit damage by rodents, as noted on *Q. pubescens* seedlings at the beginning of the experiment, but this protective effect was not investigated here, and deserves further work.

4.3 Plant stress: leaf potential and F_v/F_m

Plant stress was measured using leaf water potential and photoinhibition values as indicators. Lower leaf water potentials were found lower under the closed than under the more open pine canopies, in line with previous studies (Rodríguez-Calcerrada et al., 2007, 2008, Robson et al., 2009), but at variance with the higher soil water content recorded in the closed shelterwoods during the summer period. The beneficial effects of wetter soil in such conditions did not therefore outweigh the negative effects of reduced light availability. The low light environment in the closed stands leads to carbon limitation and probably an enhanced biomass allocation to shoots rather than roots compared with a higher light environment (e.g. McConnaughay and Coleman, 1999). Limited growth, probably unfavourable biomass allocation and stronger competition by pine roots (Ricard et al., 2003) could result in a lower capacity of seedling to face summer drought in dense pinewoods. In a previous experiment conducted in central Spain on *Quercus* seedlings planted below a dense *P. sylvestris* L. stand and a medium canopy gap, Rodríguez-Calcerrada et al., (2008) found a higher degree of water stress (i.e. lower pre-dawn leaf water potentials) in the seedlings of the dense stand despite similar soil moisture contents in both sites.

related to photoinhibition, i.e. reduction of the photosynthetic capacity (Farquhar et al., 1989). For both oak species, F_v/F_m values remained high (above 0.75), indicating a relatively mild photoinhibition, and showed a decrease during the summer season. This decrease was probably due to water stress, as the values increased again after the first major rainfall. Reduction of F_v/F_m can result from different types of stress acting alone or combined, and previous studies have shown that water stress can enhance photoinhibition, although its effects are species-specific, year- and season-dependent and vary with the type of leaf monitored and the time of day (e.g. Prietro et al., 2009; Valladares and Pearcy 1997). Photoinhibition in *Q. ilex* seedlings was highest in the light shelterwoods where light availability was highest and lowest in the other treatments. In Mediterranean environments, increasing light intensities usually overstretch the capacity for orderly energy dissipation by the photosynthetic system, resulting in enhanced photoinhibition (Long et al., 1994). However, this explanation does not hold for *Q. pubescens*, as photoinhibition was higher in the darker environment. This difference between the two oaks may arise because the *Q. pubescens* was subjected to more severe water stress in closed stands. Méthy et al. (1996), studying photochemical efficiency (F_v/F_m) of *Q. ilex* and *Q. pubescens* to drought showed that F_v/F_m decreased sharply with predawn leaf water potential < 4 Mpa. Below potentials of -4 to -4.5 Mpa, *Q. pubescens* underwent more severe damage than *Q. ilex*, probably because of greater sensitivity to cavitation (Damesin et al., 1998; Tyree and Cochard, 1996). Higher water stress, in addition to lower tolerance to shade, could thus explain the contrasting behaviour of the deciduous *Q. pubescens* compared with the evergreen *Q. ilex*.

5. Conclusion

Our results suggest that the growth – and to a lesser extent the survival – of the two co-occurring Mediterranean oak species are mainly driven by light availability under shelterwoods. However, it would be too easy and too early to conclude that light shelterwoods

(i.e. heavily thinned stands) are to be preferred to denser ones in all situations. Our results show that light shelterwoods also lead to lower soil water content during the summer period and to enhanced growth of the ground vegetation. Seedlings were not impacted by such detrimental factors, i.e. less soil water availability and more competition by vegetation, but this finding is mitigated by at least two considerations. First, the positive effect on height growth of the shrub vegetation has to be considered in the light of the moderate development of the shrub vegetation three years after thinning. In subsequent years, shrub vegetation is likely to develop faster and so could affect seedling growth negatively. Also, in the presence of more competitive species such as grasses (e.g. *Brachypodium retusum* in our area), strong development of the ground vegetation under light shelterwoods could be more detrimental to the underplanted seedlings than recorded in this study (Prévosto et al., 2010). Second, the three years of this study were ‘wet’ years and therefore not representative of the general Mediterranean climate, in which ‘dry’ years are usually considered as major bottlenecks for the vegetation dynamics.

Observations over longer periods are thus needed to determine whether the beneficial effects on seedling development provided by light shelterwoods are lasting, or whether intermediate situations are to be preferred, as usually advocated in the literature (Gómez-Aparicio et al., 2009; Paquette et al., 2006).

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Table 1. Stand dimensions, light values and vegetation covers (mean value, SD in brackets) for the three treatments. Shrub height and cover values are given 3 years after treatment application. Letters indicate statistical differences between treatments ($P < 0.05$, Tukey test).

Treatment	Basal area (m ² /ha)	Pine density (N/ha)	Pine girth (cm)	Light trans. (%)	R:FR ratio	Blue light ratio	Shrub height (cm)	Shrub cover (%)	Herb cover (%)	Litter cover (%)
Light shelterwood	10.2 a (0.90)	196 a (63)	81.6 a (15.0)	52.2 a (0.10)	1.42 a (0.05)	0.57 a (0.04)	67 a (26)	45 a (12.9)	<1%	68.3 a (17.1)
Medium shelterwood	19.2 b (0.68)	576 b (29)	61.5 b (1.56)	33.2 b (0.04)	1.22 b (0.03)	0.38 b (0.02)	56 b (28)	25 b (5.8)	<1%	76.9 a (6.0)
Dense shelterwood	32.0 c (3.87)	1664 c (448)	45.5 c (2.9)	13.1 c (0.02)	1.13 b (0.01)	0.26 c (0.01)	36 c (23)	7 c (2.1)	0	78.2 a (4.1)

Figure captions

Figure 1. Number of seedlings per sowing point (mean \pm SE) against time since emergence (time 0 = June 2008). Open circles: Light Shelterwood, grey circles: Medium Shelterwood, black circles: Dense Shelterwood. Letters indicate statistical differences for the last date between treatments ($P < 0.05$, Nemenyi test).

Figure 2. Soil water content during years 2009 (April–October) and 2010 (May–November) at two depths for the three treatments: Light Shelterwood (open circles), Medium Shelterwood (grey circles) and Dense Shelterwood (black circles). Rainfall values are indicated by vertical black bars. Arrows indicate significant differences between treatments for a given date ($P < 0.05$, Kruskal-Wallis test)

Figure 3. Soil temperatures measured at three dates in the three treatments. Letters indicate differences between treatments (Tukey test, $P < 0.05$). LS: light Shelterwood, MS: Medium Shelterwood, DS: Dense Shelterwood.

Figure 4. Dimensions of the 3-year old oak seedlings for the three treatments (mean values + SE) A) seedling stem base diameter, B) seedling height, C) height / stem diameter ratio. White bars correspond to *Q. pubescens* and black bars to *Q. ilex*. Letters indicate significant differences ($P < 0.05$) between treatments for a given oak species (Tukey test). DS: dense shelterwood, MS: medium shelterwood, LS: light shelterwood

Figure 5. Influence of shrub cover in classes on height for the Medium Shelterwood and Light Shelterwood treatments (mean \pm SE). Black circles refer to *Q. ilex* and white circles to *Q. pubescens*. In each treatment, influence of shrub cover classes on height for a given species is indicated by P value.

Figure 6. F_v/F_m ratio (mean \pm SE) measured at different dates during summer and early autumn 2009 for A) *Q. pubescens* B) *Q. ilex*. Treatments: Light Shelterwood (open circles), Medium Shelterwood (grey circles) and Dense Shelterwood (black circles). Stars indicate statistical differences between treatments (Kruskal-Wallis test): $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***), NS: not significant.

Figure 7. Leaf predawn potential at two dates for *Q. pubescens* (white bar) and *Q. ilex* (grey bar) by treatment. LS: light Shelterwood, MS: Medium Shelterwood, DS: Dense Shelterwood. Letters indicate significant differences between treatments for a given species ($P < 0.05$, Tukey test)

Fig. 1

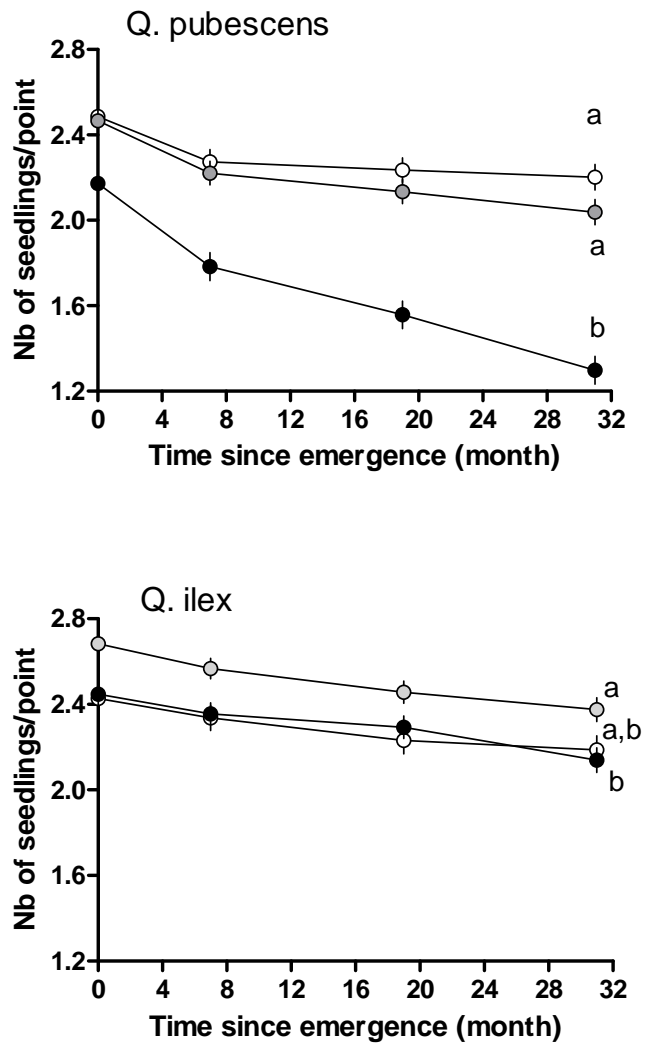


Fig. 2

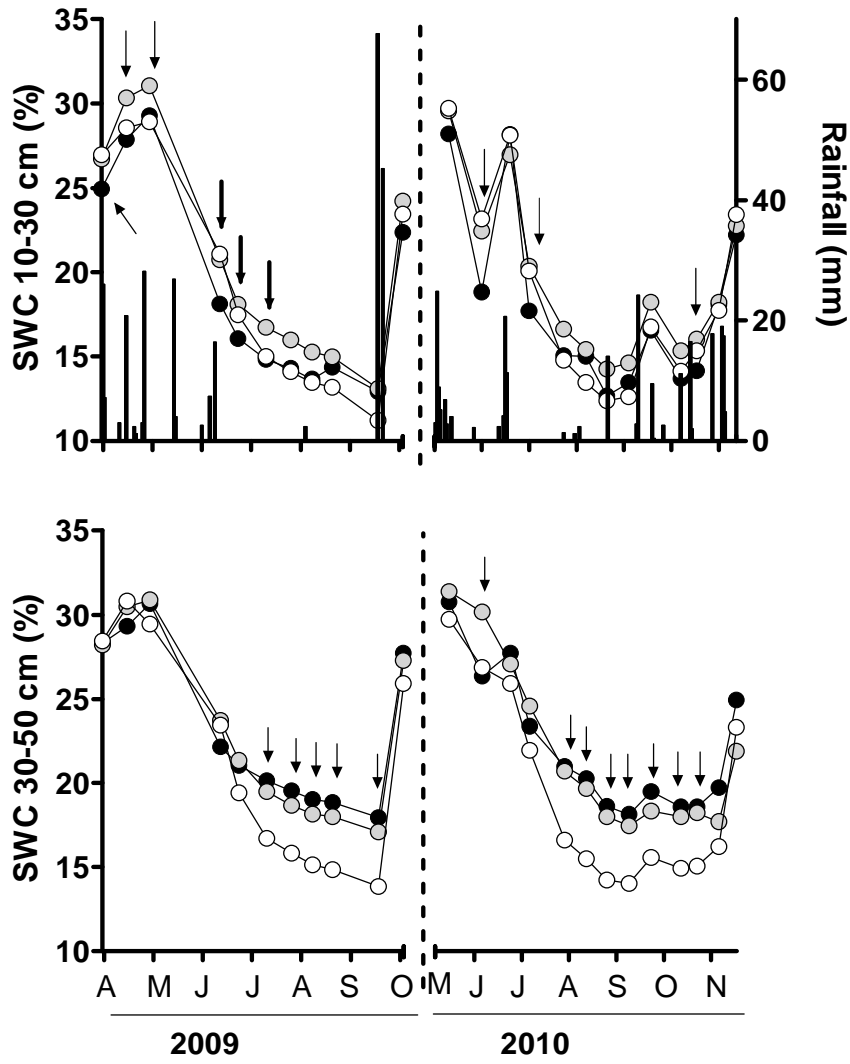


Fig. 3

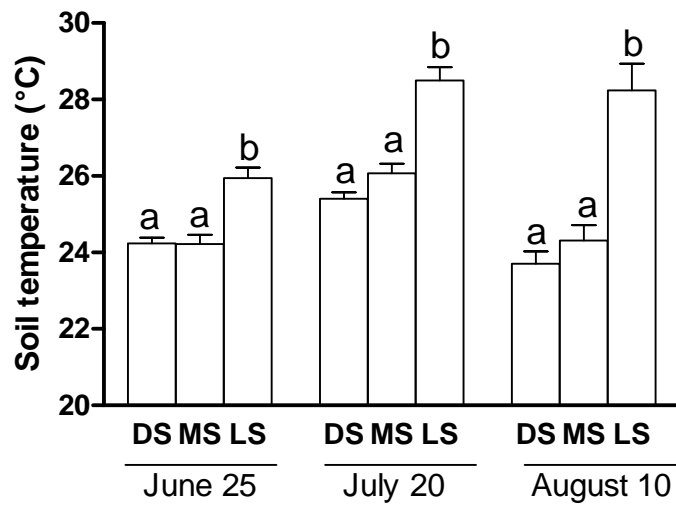


Fig. 4

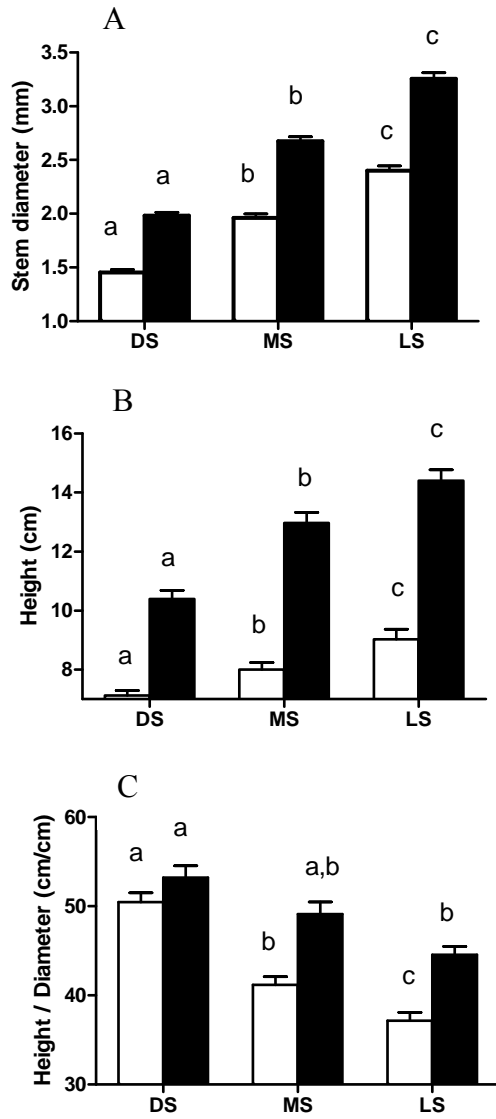


Fig. 5

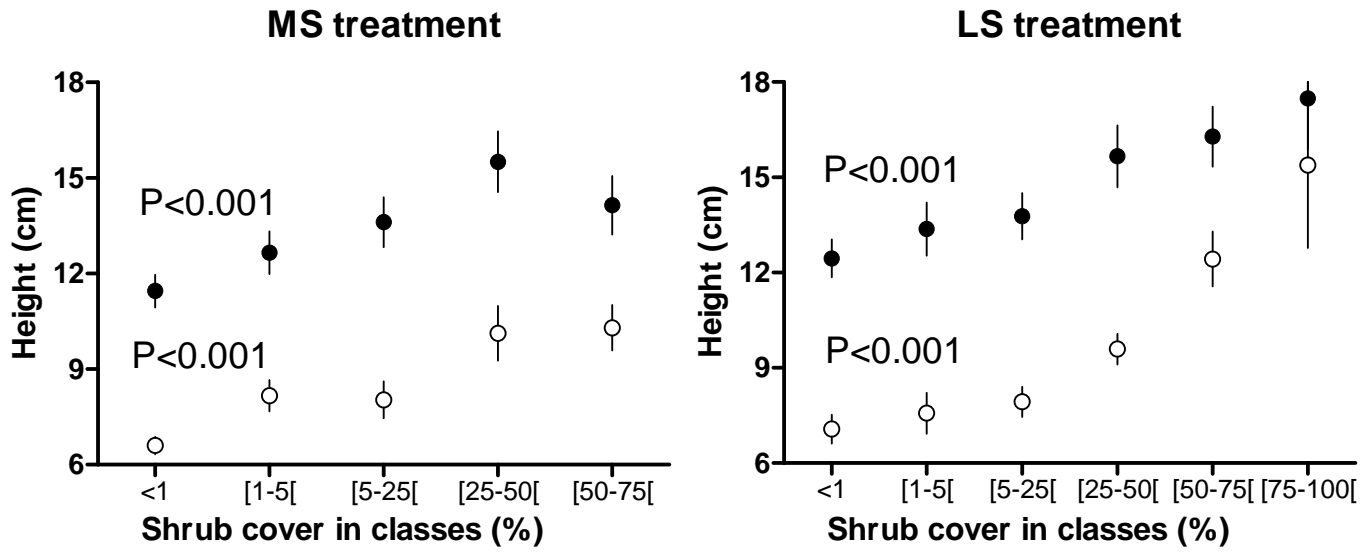


Fig. 6

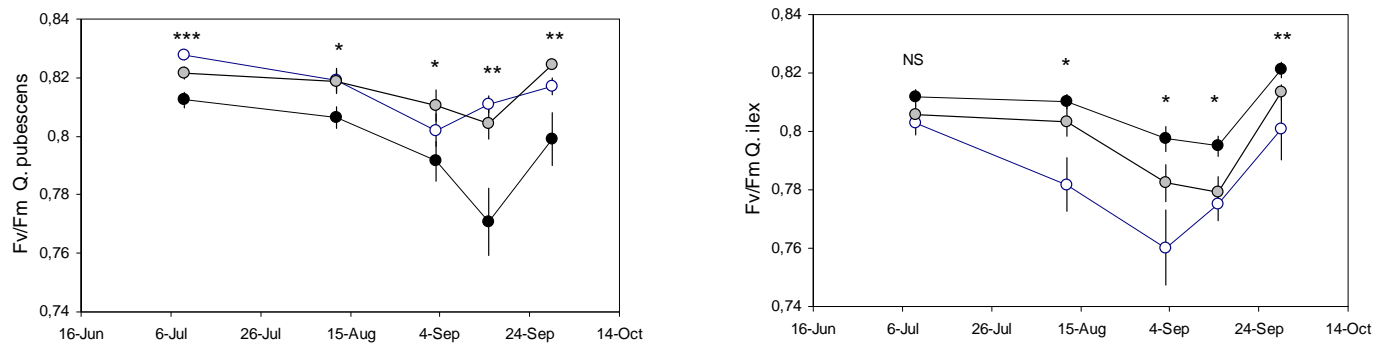


Fig. 7

