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Influence of overstory density on understory light, soil moisture, and survival of two underplanted oak species in a Mediterranean montane Scots pine forest

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Abstract

Information of tree-nurse shelterwood effects on survival of underplanted seedlings is particularly scant in Mediterranean forest ecosystems. To study light and water resources availability and survival associated to overstory density, two-year-old seedlings of *Quercus petraea* (Matt.) Liebl. (sessile oak) and *Quercus pyrenaica* Willd. (pyrenean oak) were planted in the understory of an even-aged Scots pine (*Pinus sylvestris* L.) plantation located in central Spain, which had been previously assigned to three density treatments: uncut, 33% thinned and 50% thinned of the original density, each replicated four times. Soil moisture was measured with a TDR during the first growing season after planting. Light conditions were estimated by hemispherical photography. Survival was measured at the end of the first growing season in the field and at the beginning of the next two growing seasons. The reduction in density after thinning had a positive effect on light availability and on near-surface soil moisture. Pyrenean oak had higher survival rates than sessile oak, which showed similarly high mortality rates in all three overstory treatments. Thinning had a positive effect on the survival of pyrenean oak, though irrespective of the intensity. Overall, these results point to the necessity to reduce canopy tree density in Mediterranean mountain pinewoods before carrying out enrichment plantations beneath.

Key words: thinning, underplanting, drought, sessile oak, pyrenean oak.

Resumen

Influencia de la espesura de un pinar albar (Sistema Central, España) en la disponibilidad de luz y agua en el sotobosque, y la supervivencia de robles plantados en su interior

Con el fin de estudiar el efecto de la espesura de la cubierta forestal en la disponibilidad de luz y agua para las plantas y su supervivencia, se plantaron brinzales de dos savias de *Quercus petraea* (Matt.) Liebl. (roble albar) y *Quercus pyrenaica* Willd. (melojo) en el interior de un pinar de *Pinus sylvestris* L. (pino albar) situado en el NE de la provincia de Madrid sometido previamente a tres tratamientos: clara del 33% de la densidad original, clara del 50% y ausencia de clara. Se midió la humedad volumétrica del suelo con un TDR y la disponibilidad de luz en el sotobosque por medio de fotografias hemisféricas. La supervivencia se midió al final del primer año y al comienzo del verano de los dos años siguientes. La reducción de la densidad del dosel incrementó la luz disponible en el sotobosque, la humedad de los primeros 10 cm de suelo y la supervivencia de las plantas de melojo, aunque no se apreció un efecto diferente segun la intensidad de la clara aplicada. La mortalidad de las plantas de roble albar fue elevada en todos los tratamientos, y superior a la del melojo. Estos resultados apuntan a la necesidad de reducir la espesura del pinar albar en la zona de estudio antes de llevar a cabo plantaciones con melojo en su interior.

Palabras clave: claras, plantaciones bajo cubierta arbórea, sequía, roble albar, melojo.

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Introduction

In the Mediterranean basin, intense land-use over millennia has led to a strong loss of forest cover (Grove and Rackham, 2001). Active reforestation programs were carried out during the twentieth century to progressively restore it, mainly for soil and watershed protection. In Spain, as a first step in this process, conifer species were widely planted in degraded lands due to their higher establishment success than less frugal broadleaved species (Pausas *et al.*, 2004; Pardo and Gil, 2005). The ultimate aim of many of those reforestations was the long-run transformation of these secondary pure even-aged coniferous stands into mixed forests or broadleaved forests (Ceballos, 1939), although this purpose has been commonly ignored afterward due to lack of funding. Therefore, currently there are more than three million hectares of pine forests whose transformation is still pending (Manuel and Gil, 1998). At present, environmental as well as social appreciation of native broadleaf forest ecosystems have recovered the interest of the transformations, namely in or around protected areas.

However, while shelterwood regeneration method is one of the most common permanent-cover techniques used in temperate forests, few experiences have dealt with nurse-tree canopy effects on understory plantations in Mediterranean ecosystems (Aranda *et al.*, 2001, 2004; Maestre *et al.*, 2003; Bellot *et al.*, 2004) and appropriate recommendations are uncertain. When light is the main limiting factor, a closed canopy often hinders establishment of seedlings of different shade-tolerances (Mass-Hebner *et al.*, 2005; Paquette *et al.*, 2006), requiring its gradual opening by means of thinnings or the creation of gaps. But owing to recurrent and severe episodes of drought during summer in Mediterranean forests, the question remains whether initial thinning might result in excessive evaporation and mortality or rather enhance soil moisture by diminishing rain interception and transpiration of the overstory (Aussenac, 2000). To a large extent, the outcome of the canopy-understory relation seems to be mediated by the effect that shade has on the conservation of soil moisture and the ability of seedlings to respond to water stress. But facilitation is an issue of active debate (Lortie and Callaway, 2006; Maestre *et al.*, 2006), as it is likely depending on the ecological features of the target species (e.g. differing tolerance to late frosts in temperate forests or to drought or excessive light in Mediterranean areas) and/or the environmental characteristics of the site (e.g. fertility or aridity).

In this context, the present study compares the effects of two thinning intensities and a control treatment in a mature Scots pine stand on the survival of underplanted seedlings of two oaks, namely the deciduous sessile oak [*Quercus petraea* (Matt.) Liebl.] and the marcescent pyrenean oak (*Quercus pyrenaica* Willd.). The former is protected in the studied Mediterranean mountain area lying north of Madrid, where it reaches one of its southernmost populations in a mixed beech-oak forest called the «El Hayedo de Montejo» forest (Gil *et al.*, 1999). Sessile oak is more susceptible to drought and high light than the Mediterranean pyrenean oak, whose ecological requirements are plainly met in the studied area (Allué, 1990). A dynamic conservation management of this reduced population requires its expansion in order to reduce its vulnerability to future environmental threats; investigation of most appropriate plantation sites is central to this end. The hypotheses of this study were (i) that mortality would be higher in sessile oak than in pyrenean oak, and (ii), that seedling mortality would be higher in the un-thinned plots because of a multiple reduction in resources.

Material and Methods

Acorns of sessile oak and pyrenean oak were collected in 2002 in the «El Hayedo de Montejo» forest and seeded the following spring in 300-cc Forest pots containing a mixed peat/vermiculite substrate (3v/1v). The substrate was enriched with slow-release fertilizer at a dosage of 2.5 g l^{-1} [Osmocote Plus (8-9 months)]. At the beginning of 2004, seedlings were transplanted to 3,000-cc Forest pots containing the same substrate type and fertilizer dosage, and maintained in partial shade (30-40% of full sunlight) in the «Puerta de Hierro» forest nursery, Madrid. In spring 2005, a total amount of 996 individuals of sessile oak and 498 individuals of pyrenean oak were outplanted under an even-aged, 42-year-old Scots pine stand. The stand is at 1,600 m elevation, in the Spanish Central System (3°30'26"W, 41°06'25"N; Fig. 1), SE-NE facing and moderately sloping (10-20%); with an almost closed canopy cover, as no thinning was made since planting. Mean density and basal area measured in 2004 were 947 ha^{-1} and 55 m^2 ha^{-1}, respectively; mean diameter (dbh) was 27.2 cm; and mean dominant height was 15 m. Understory vegetation was sparse, mainly of *Pteridium*

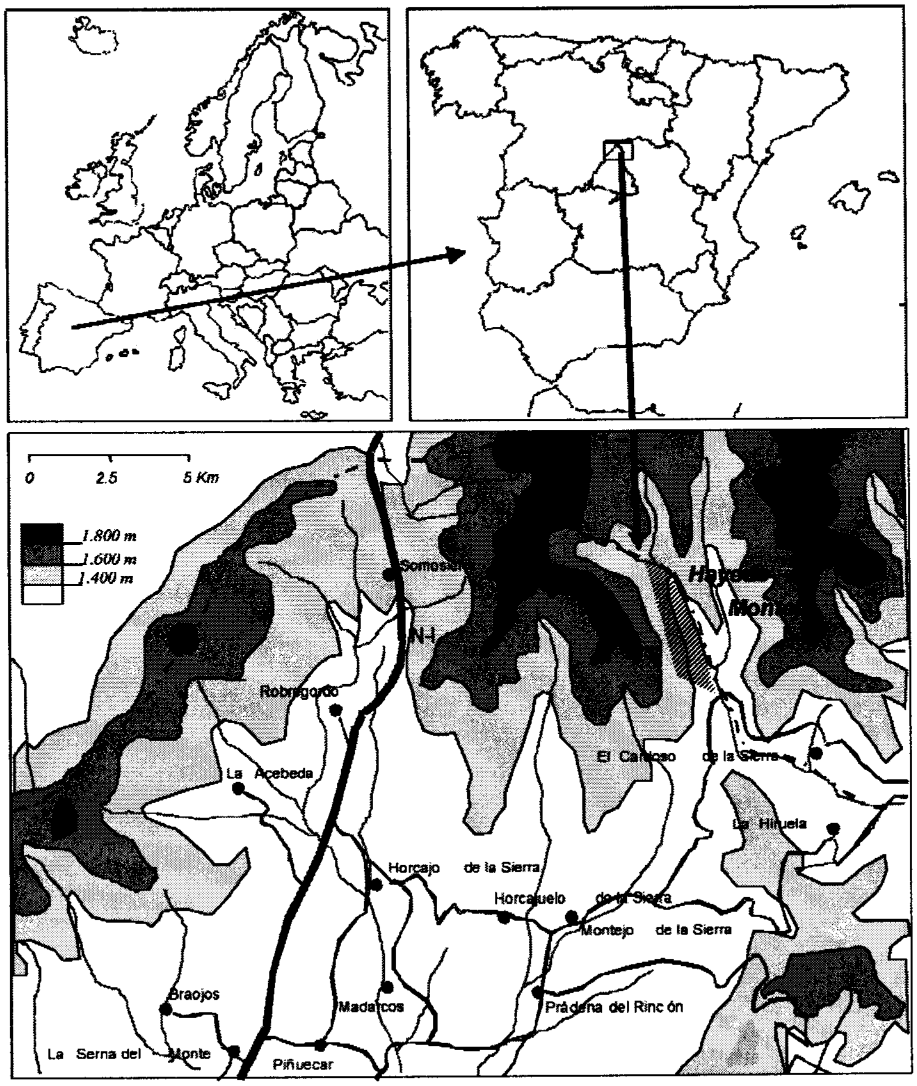

Figure 1. Location of the experimental site, marked with an «X», up-slope of the «El Hayedo de Montejo» forest.

aquilinum L. (Kuhn) and *Ilex aquifolium* L. A soil pit dug out in the stand revealed that roots of Scots pine trees were abundant between 0-15 cm, frequent up to 40 cm and scant at deeper horizons. Soil depth ranges from 70 to at least 100 cm, though the soil becomes stony below 60 cm. The soil is a distric cambisol (FAO classification) developed on gneiss bedrock, mildly acid (pH-H_2O: 5.95), and fertile (8.2% organic matter; 0.4% total N content and 112 ppm K in the shallower 15 cm). It is well-drained [permeability index of Gandullo (1985): 5] and has an adequate water-holding capacity (170 mm m^{-1} averaged across soil horizons and 100 mm for the whole profile; following equations in Domingo-Santos *et al.*, 2006), similar to nearby soils [e.g. 148 mm m^{-1} (164 mm) in pyrenean oak-dominated stands and 142 mm m^{-1} (229 mm) in holly-dominated stands; Alonso, 2001]. The climate is sub-Mediterranean, with a period of water-shortage; mean annual rainfall is 1,124 mm and mean annual temperature is 8.7°C (Fig. 2). According to Allué (1990) phytoclimate is Nemoromediterranean [type $VI(IV)_2$], cool (mean of coldest month: 0.4°C) and sub-humid (with drought in July and August).

In the year before planting two thinning treatments had been applied to the stand cutting 33 and 50% of the original density (Table 1); felled trees were removed from the site and the area (10 ha) was further surrounded with a 1.5-m height wire fence. These thinning intensities corresponded with a reduction of Reineke's Stand-Density Index (SDI) from 1,100 in the uncut

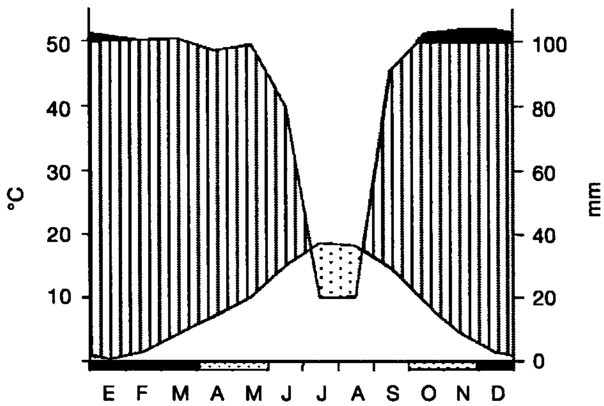

Figure 2. Climatic diagram for the study area. *Source:* Gandullo *et al.*, 1977.

control treatment, *i.e.* 76% of the maximum SDI (1,445 for un-thinned Scots pine stands in Spain according to Río *et al.*, 2001), to 780 and 600, about 54% and 42% of the SDI_{max}, respectively. Four complete blocks were distributed along an N-S gradient in a split-plot design, with overstory treatment (uncut, 33% thinned, 50% thinned) as the main plot factor, and the species (pyrenean oak and sessile oak) as the subplot factor. An experimental plot (*c* 0.053 ha) was established at the centre of each strip. Plots 1-3 in block I contained 80 individuals of sessile oak and 40 individuals of pyrenean oak each, planted 1.5-m-separated in two rows among the pine rows. Plots 4-12 (blocks II to IV) contained 84 individuals of sessile oak and 42 individuals of pyrenean oak each, planted 1-m-separated in one row among the pine rows. This different planting design was due to a different spacing of pine trees in Block 1 (5 m between rows) *vs.* the rest (3.5 m).

Current precipitation and temperature in the study area were recorded by means of a rain gauge (1-hour interval) and a temperature sensor (1-min interval), respectively, both connected to a data-logger. The sensors are placed at the top of a nearby 16-m height tower. It is operating since 1995 although data from 1999 and 2001-2002 were missing, due to the rising of the top part over the uppermost canopy. Volumetric soil water content was measured in summer 2005 with a TDR (Trase System I, Soil Moisture Equipment Corp. USA) inside one PVC-tube buried in the center of each plot, for a total of 12 tubes. Light availability was estimated with hemispherical photographs. Five digital photographs (Nikon Coolpix 4500) were taken at seedling height in late summer 2005, in the centre and corners of a *c* 10-m-side square located in the middle of each plot. Photographs were analyzed with Hemiview 2.1 Canopy Analysis Software, quantifying the Global Site Factor index (GSF). Survival was assessed at the end of the first growing season in the field (October 2005), and in the beginning of the two following growing seasons (June 2006 and June 2007).

The survival of each species under the three treatments was analyzed by a logistic regression model, taking into account the four replicates (blocks) as categorical predictor variable and the basal area (BA) after thinning as covariable characterizing the thinning. In an alternative approach, the correlated GSF was used in place of BA. The soil water contents on different depths and dates were used as additional variables for exploratory data analysis. General linear models were run to test for the significance of treatment effects on light and soil moisture, further using the Tukey's HSD test to separate means (at $P < 0.05$). The relationships between BA with light and soil moisture were explored by Pearson's correlation coefficients.

Results

Both 2005 and 2006 summers were warmer and drier than average, especially 2005 (Table 2).

GSF differed significantly between the un-thinned and thinned plots, but hardly at all between both thinning levels ($P < 0.001$) (Table 1). Soil moisture averaged over summer months was lower in the uncut treatment than in the two thinning treatments ($P < 0.01$). For all plots, GSF correlated negatively with the residual BA

Table 1. Mean values (± SE) of basal area (BA), tree density, light availability (GSF) and soil moisture (0-40 cm depth) averaged over the summer months of 2005 in each treatment

Overstory	*n*	BA (m^2 ha^{-1})	Density (ha^{-1})	*n*	GSF (%)	*n*	Soil moisture (%)
Uncut	4	54.8 ± 1.4	947 ± 84	20	16.3 ± 0.6	4	14.0 ± 0.8
33% thinned	4	40.1 ± 1.3	658 ± 16	20	25.8 ± 0.7	4	15.7 ± 1.4
50% thinned	4	30.5 ± 0.5	446 ± 18	20	26.8 ± 0.9	4	17.0 ± 0.4

Table 2. Precipitation and mean temperature in the study area over the summer months (June to September) of 2005 and 2006

Year	P (mm)	T (°C)
2005	40.4	17.7
2006	112	17.3
Average[1]	143.2	16.9
Average[2]	168.2	16.6

[1] Averages from our meteorological tower between 1995 and 2006 (data of 1999, 2001 and 2002 were missing). [2] Averages estimated for the study area from precipitation- and temperature-altitude regression lines constructed from data recorded between 1955 and 1969 (Gandullo *et al.*, 1976).

left after thinning (Fig. 3). A negative correlation was also found between the residual BA and the soil moisture at 10 cm depth (Fig. 3).

The survival of sessile oak was poor in all plots (Fig. 4), though being somewhat higher in the first block, with a wider between-row distance of the original pine stand. Overall, there was no significant effect of thinning, light environment or soil-water content on the survival of sessile oak. In pyrenean oak, survival was significantly higher in the thinned plots (Fig. 4), though with strong differences between blocks. Therefore, the logistic regression model for survival in all three dates included as significant factors Block and Treatment, though since effects of both thinning intensities did not differ significantly among each other, they can be pooled into a common level of a new variable «thinned/unthinned» that explains practically the same proportion of deviation ($D_{\%}$ 67.34 *vs.* 67.98% for the last date) with a lower mean square error (MSE

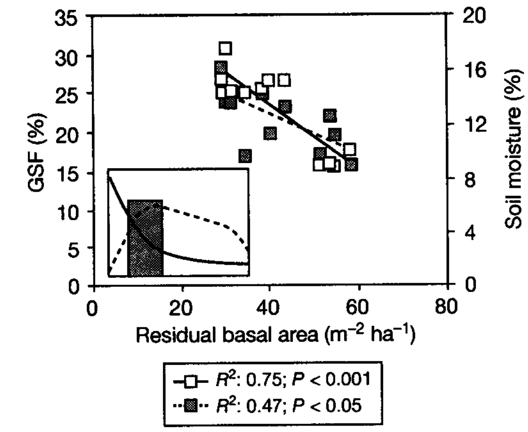

Figure 3. Variation of light (GSF; white squares, continuous line) and summer average soil moisture at 10-cm depth (grey squares, dashed line) with the residual basal area in all plots. The inset represents the predicted evolution of light and soil moisture with basal area based on previous works (see references in text); the shady area indicates a possible range of basal area to be targeted.

0.167 *vs.* 0.186). The BA after thinning as environmental proxy of each plot for fixed treatment effects matched plainly the adjustment of the original model ($D_{\%}$ 67.29%; MSE 0.152 in 2007) or even improved it slightly ($D_{\%}$ 69% *vs.* 67% in 2005, 63% *vs.* 61% in 2006) whereas the light environment GSF performed worse (*e.g.* $D_{\%}$ 54%; MSE 0,270 in 2007). As the ratios of deviance, scaled deviance, Pearson Chi-Square and Scaled Pearson Chi-Square to the respective degrees of freedom were in all cases close to 1.0, there was no evidence of over-dispersion. The use of soil water content at any depth as covariable, either did not improve the model or it did introduce correlations between estimations of

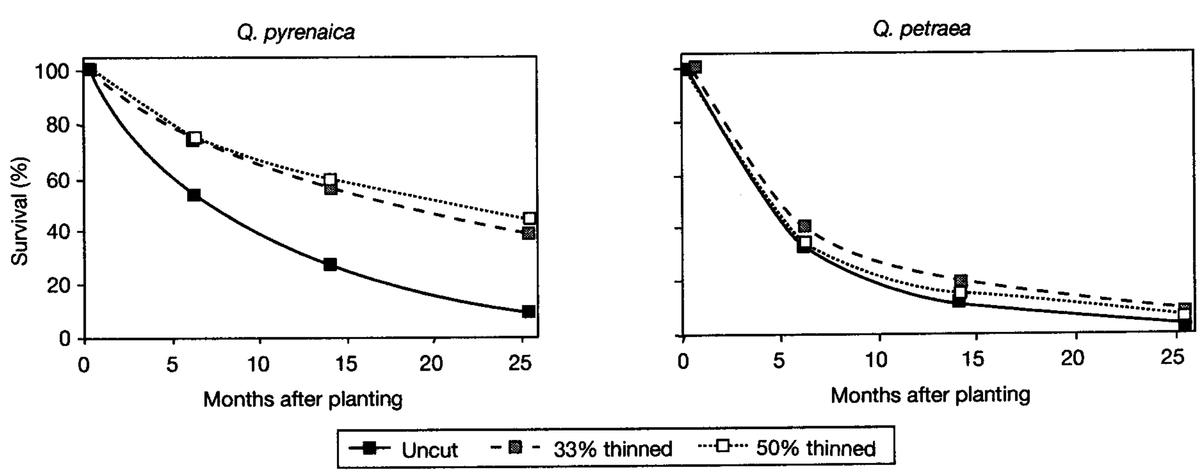

Figure 4. Cumulative survival of seedlings of pyrenean oak and sessile oak for the three treatments.

model coefficients that imply collinearity, therefore, they were discarded.

The fence proved useful to deter cattle, but not deers, from entering the enclosure. We observed symptoms of deer browsing on most seedlings already in the first year (≈95% of seedlings damaged); independently of the overstory density ($P > 0.15$), but not of the species (91% in pyrenean oak *vs.* 96% in sessile oak; $P < 0.001$). Well-fertilized and neatly-lined-up seedlings might be particularly prone to browsing during the harsh summer of 2005.

Discussion

Our results confirmed that overstory density influences both light available in the understory and soil moisture. The observed small effect of thinning of ~30% and ~50% in BA and density, respectively, on the GSF, is congruent with the non-linear relationship between light availability and BA referred in other works (Hale *et al.*, 2004; Lapointe *et al.*, 2006). Thinning of dense stands do not produce big gaps and have thus little impact on light, while small changes in already low-BA stands have profound effects opening the canopy. The relationship of soil moisture with basal area seems less straightforward, due to a stronger influence of climatic and edaphic factors. The examination of experiences concerning tree or shrub effects on the microenvironment in Mediterranean ecosystems lead us to expect a non linear relationship of moisture with density (Fig. 3), derived mainly from the changing interplay among evaporation, water uptake by both canopy and understory vegetation, and rainfall interception (Joffre and Rambal, 1993; Holmgren *et al.*, 1997; Castro *et al.*, 2004; Maestre *et al.*, 2004; Gómez-Aparicio *et al.*, 2005; Rey-Benayas *et al.*, 2005, but see Bellot *et al.*, 2004). The negative, linear correlation of moisture at 10-cm depth against the observed range of residual basal area suggests that increased understory light after thinning of the tree-canopy did not cause too intense evapotranspiration as to offset the reduction in living fine roots of Scots Pine in the upper soil layers and/or a likely increase in throughfall precipitation (Kozlowski *et al.*, 1991). Nonetheless, given the trade-offs in plant acclimatory responses to light and soil moisture resources (see Sack and Grubb, 2002), experiments should also aim to discern whether regeneration silvicultural practices should target initial density levels at which soil moisture is maximized or rather at which both light and soil moisture resources are optimized (see inset of Fig. 3).

The clear light-related response to thinning in pyrenean oak in terms of survival contrasted with the generalized outplanting failure of sessile oak possibly owing to the severe drought of 2005. Survival of pyrenean oak was higher in thinned than in uncut plots probably in relation with the associated increase in soil moisture and light. Small increases in soil water content can greatly affect the plant water potential, whereas small increases in light can have profound effects on the photosynthetic capacity and can be sufficient to reach maximum values of photosynthetic capacity in shade-tolerant species (Gardiner *et al.*, 2001; Rodríguez-Calcerrada *et al.*, 2007a). In turn, increased carbon gain may result both in a greater capacity to withstand water stress (Augé *et al.*, 1990) and to develop new roots after outplanting (Grossnickle, 2005), resulting in a better establishment. Higher drought-tolerance features of pyrenean oak could also have been negative for its successful in more shaded plots. According to Reich *et al.* (1998), high photosynthetic rate, typical of this species, can imply a high respiration rate, which together with its high root to shoot ratio, could negatively affect carbon balance and thus survival in the lower-light plots. This could be particularly so in situations of severe water stress, as it was experienced during this study, since respiration remains less affected by water stress than photosynthesis (Ribas-Carbo *et al.*, 2005).

Overall lower survival of sessile oak than pyrenean oak is consistent with the more drought-sensitive features of the former (Aranda *et al.*, 1996; Rodríguez-Calcerrada *et al.*, 2007a). Besides, the greater root to shoot ratio of seedlings of pyrenean oak, together with their higher resprouting ability (Rodríguez-Calcerrada *et al.*, 2007b) could have enhanced their resistance to browsing damages over those of sessile oak. In line with this reasoning, despite browsing was similar among overstory treatments, different light availability for plants between treatments could have influenced resilience of seedlings of pyrenean oak to foliage removal (Baraza *et al.*, 2004). Higher light in the thinned plots likely allowed for a higher leaf area re-development and carbon gain revenue with respect to the uncut plots, which could help to rebuild-up non-structural carbohydrate reserves in the root system and favour initial persistence, at least until reserves are depleted in repeatedly producing new shoots to compensate for the continued lost of foliage (Baraza *et al.*, 2004; Landhäusser and Lieffers, 2002).

Conclusions

Our results suggest that overstory reduction by means of thinning might be advisable to foster artificial oak regeneration in Mediterranean humid mountains, as seems to be a general pattern in other biomes (Paquette *et al.*, 2006), given the observed increases in survival of pyrenean oak seedlings, light and soil moisture in the thinned treatments with respect to the denser, uncut treatments. Weak thinning-induced variations in understory conditions (light and soil moisture) up to 50% removal possibly made that no difference in survival between the two thinning levels was observed. While the role of shrubs in the success of tree plantations in Mediterranean ecosystems is receiving considerable attention (e.g. Pérez-Devesa *et al.,* 2008), less is being paid to the role of established tree stands; more research on this topic is clearly needed.

Acknowledgements

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References

ALLUÉ ANDRADE J.L., 1990. Atlas fitoclimático de España. Monografías INIA 69. Ministerio de Agricultura, Madrid.

ALONSO NÁGER J., 2001. Inventario forestal del Sitio Natural de Interés Nacional «Hayedo de Montejo de la Sierra», monte nº 89 del CUP «El Chaparral y la Solana» (Comunidad de Madrid). Proyecto de fin de carrera. EUIT Forestal, Madrid. Inédito.

ARANDA I., GIL L., PARDOS J.A., 1996. Seasonal water relations of three broadleaved species [*Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl and *Quercus pyrenaica* Willd] in a mixed stand in the centre of the Iberian Peninsula. For Ecol Manage 84, 219-229.

ARANDA I., GIL L., PARDOS J.A., 2001. Effects of thinning in a *Pinus sylvestris* L. stand on foliar water relations of *Fagus sylvatica* L. seedlings planted within the pinewood. Trees 15, 358-364.

ARANDA I., GIL L., PARDOS J.A., 2004. Improvement of growth conditions and gas exchange of *Fagus sylvatica* L. seedlings planted below a recently thinned *Pinus sylvestris* L. stand. Trees 18, 211-220.

AUGÉ R.M., STODOLA A.J.W., PENNELL B.D., 1990. Osmotic and turgor adjustment in *Rosa* foliage drought-stressed under varying irradiance. J Amer Soc Hort Sci 115, 661-667.

AUSSENAC G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann For Sci 57, 287-301.

BARAZA E., GÓMEZ J.M., HÓDAR H.A., ZAMORA R., 2004. Herbivory has a greater impact in shade than in sun: response of *Quercus pyrenaica* seedlings to multifactorial environmental variation. Can J Bot 82, 357-364.

BELLOT J., MAESTRE F.T., CHIRINO E., HERNÁNDEZ N., DE URBINA J.O., 2004. Afforestation with *Pinus halepensis* reduces native shrub performance in a Mediterranean semiarid area. Acta Oecol 25, 7-15.

CASTRO J., ZAMORA R., HÓDAR J.A., GÓMEZ J.M., 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J Ecol 92, 266-277.

CEBALLOS L., 1939. Plan general para la repoblación forestal en España. Icona, Madrid.

DOMINGO SANTOS J.M., FERNÁNDEZ DE VILLARÁN SAN JUAN R., CORRAL PAZOS DE PROVENS E., RAPP ARRARÁS I., 2006. Estimación de la capacidad de retención de agua en el suelo: revisión del parámetro CRA. Invest Agrar: Sist Recur For 15, 14-23.

GANDULLO J.M., SÁNCHEZ-PALOMARES O., GONZÁLEZ-ALONSO S., 1976. Contribución al estudio ecológico de la sierra de Guadarrama – II clima. An INIA Ser Recursos Naturales 2, 23-36.

GANDULLO J.M., SÁNCHEZ-PALOMARES O., SERRADA R., 1977. Estudio climático y edafológico del monte «El Chaparral y La Solana» propiedad de Montejo de la Sierra. Congreso de Biogeografía, Guadarrama, Madrid. Inédito.

GANDULLO J.M., 1985. Ecología vegetal. Fundación Conde del Valle de Salazar, Madrid.

GARDINER E.S., SCHWEITZER C.J., STANTURF J.A., 2001. Photosynthesis of Nuttall oak (*Quercus nuttallii* Palm.) seedlings interplanted beneath an eastern cottonwood (*Populus deltoides* Bartr. Ex Marsh.) nurse crop. For Ecol Manage 149, 283-294.

GIL L., PARDO F., ARANDA I., PARDOS J.A., 1999. El Hayedo de Montejo: pasado y presente. Comunidad de Madrid, Madrid.

GÓMEZ APARICIO L., GÓMEZ J.M., ZAMORA R., JANIS B., 2005. Canopy *vs.* soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. J Veg Sci 16, 191-198.

GROSSNICKLE S.C., 2005. Importance of root growth in overcoming planting stress. New For 30, 273-294.

GROVE O.T., RACKHAM O., 2001. The nature of Mediterranean Europe: an ecological history. Yale University Press, London.

HALE S.E., LEVY P.E., GARDINER B.A., 2004. Trade-offs between seedling growth, thinning and stand stability in Sitka spruce stands: a modelling analysis. For Ecol Manage187, 105-115.

HOLMGREN M., SCHEFFER M., HUSTON M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78, 1966-1975.

JOFFRE R., RAMBAL S., 1993. How tree cover influences the water balance of Mediterranean rangelands. Ecology 74, 570-582.

KOZLOWSKI T.T., KRAMER P.J., PALLARDY S.G., 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego, California.

LANDHÄUSSER S.M., LIEFFERS V.J., 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. J Ecol 90, 658-665.

LAPOINTE B., BRADLEY R., PARSONS W., BRAIS S., 2006. Nutrient and light availability to white spruce seedlings in partial and clearcut harvested aspen stands. Silva Fenn 40, 459-471.

LORTIE C.J., CALLAWAY R.M., 2006. Re-analysis of meta-analysis: support for the stress-gradient hypothesis. J Ecol 94, 7-16.

MAAS-HEBNER K.G., EMMINGHAM W.H., LARSON D.J., CHAN S.S., 2005. Establishment and growth of native and conifer seedlings underplanted in thinned Douglas-fir stands. For Ecol Manage 208, 331-345.

MAESTRE F.T., CORTINA J., BAUTISTA S., BELLOT J., 2003. Does *Pinus halepensis* facilitate the establishment of shrubs in Mediterranean semi-arid afforestations? For Ecol Manage 176, 147-160.

MAESTRE F.T., CORTINA J., BAUTISTA S., 2004. Mechanisms underlying the interaction between *Pinus halepensis* and the native late-succesional shrub *Pistacia lentiscus* in a semi-arid plantation. Ecography 27, 776-786.

MAESTRE F.T., VALLADARES F., REYNOLDS J.F., 2006. The stress-gradient hypothesis does not fit all relationships between plant-plant interactions and abiotic stress: further insights from arid environments. J Ecol 94, 17-22.

MANUEL C.M., GIL L., 1998. La transformación histórica del paisaje forestal en España. Segundo Inventario Forestal Nacional 1986-1996, MMA, Madrid.

PAQUETTE A., BOUCHARD A., COGLIASTRO A., 2006. Survival and growth of under-planted trees: a meta-analysis across four biomes. Ecol Appl 16, 1575-1589.

PARDO F., GIL L., 2005. The impact of traditional land use on woodlands: a case study in the Spanish Central System. J Hist Geogr 31, 390-408.

PAUSAS J.G., BLADÉ C., VALDECANTOS A., SEVA J.P., FUENTES D., ALLOZA J.A., VILAGROSA A., BAUTISTA S., CORTINA A., VALLEJO R., 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: new perspectives for an old practice - a review. Plant Ecol 171, 209-220.

PÉREZ-DEVESA M., CORTINA J., MILAGROSA A., VALLEJO R., 2008. Shrubland management to promote *Quercus suber* L. establishment. For Ecol Manage 255, 374-382.

REICH P.B., WALTERS M.B., TJOELKER M.G., VANDERKLEIN D., BUSCHENA C., 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct Ecol 12, 395-405.

REY BENAYAS J.M., NAVARRO J., ESPIGARES T., NICOLAU J.M, ZAVALA M.A., 2005. Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. For Ecol Manage 212, 302-314.

RIBAS-CARBÓ M., TAYLOR N.L., GILES L., BUSQUETS S., FINNEGAN P.M., DAY D.A., LAMBERS H., MEDRANO H., BERRY J.A., FLEXAS J., 2005. Effects of water stress on respiration in soybean leaves. Plant Physiol 139, 466-473.

RÍO M., ROIG S., CAÑELLAS I., MONTERO G., 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For Ecol Manage 142, 79-87.

RODRÍGUEZ-CALCERRADA J., PARDOS J.A., GIL L., ARANDA I., 2007a. Acclimation to light in seedlings of *Quercus petraea* (Mattuschka) Liebl. and *Quercus pyrenaica* Willd. planted along a forest-edge gradient. Trees 21, 45-54.

RODRÍGUEZ-CALCERRADA J., PARDOS J.A., GIL L., REICH P.B., ARANDA I., 2007b. Light response in seedlings of a temperate (*Quercus petraea*) and a sub-Mediterranean species (*Quercus pyrenaica*): contrasting ecological strategies as potential keys to regeneration performance in mixed marginal populations. Plant Ecol (In press).

SACK L., GRUBB P.J., 2002. The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. Oecologia 131, 175-185.