Methods to improve the recruitment of holm-oak seedlings in grazed Mediterranean savanna-like ecosystems (dehesas)

María Leiva, Juan Mancilla-Leyton, Ángel Martín-Vicente

► To cite this version:

María Leiva, Juan Mancilla-Leyton, Ángel Martín-Vicente. Methods to improve the recruitment of holm-oak seedlings in grazed Mediterranean savanna-like ecosystems (dehesas). *Annals of Forest Science*, 2012, 70 (1), pp.11-20. 10.1007/s13595-012-0225-0 . hal-01201450

HAL Id: hal-01201450

<https://hal.science/hal-01201450>

Submitted on 17 Sep 2015

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Methods to improve the recruitment of holm-oak seedlings in grazed Mediterranean savanna-like ecosystems (dehesas)

María José Leiva · Juan Manuel Mancilla-Leyton · Ángel Martín-Vicente

Received: 15 March 2012 / Accepted: 24 June 2012 / Published online: 1 August 2012
© INRA / Springer-Verlag France 2012

Abstract

• **Context** “Dehesas” are savanna-like ecosystems of human origin that extend broadly in the Mediterranean area of the Iberian Peninsula. They consist of scattered oaks (mainly *Quercus ilex* subsp. *ballota* L. holm-oak), an annual grassland layer and interspersed shrubs. These ecosystems, used for grazing and wild game, support high plant and animal biodiversity and provide important environmental services. At present, Mediterranean “dehesas” are endangered by the lack of oak regeneration.

• **Aims** This paper analyses the efficiency of: (1) using shrubs as nurse plants; (2) drip irrigation of seedlings during summer; and (3) a combination of the two methods for the restoration of a “dehesa” in a mid-mountain Mediterranean area of southern Spain.

• **Methods** Different techniques were tested to improve the recruitment of holm-oak seedling during a 3-year field experiment: (1) acorn plantation in open spaces, irrigating seedlings during the first dry season; (2) acorn plantation beneath the canopy of *Myrtus communis* L. and (3) both methods combined.

• **Results** There was a large facilitative effect of myrtle for the recruitment of holm-oak seedlings, regardless of the supply of irrigation. This effect was associated with a large decrease in

air temperature and photosynthetically active radiation beneath myrtle canopies. By contrast, summer irrigation of seedlings planted in open spaces did not improve seedling survival after 3 years despite a small and transient positive effect on seedling survival during the 1st year.

• **Conclusion** The use of evergreen shrubs, such as myrtle, as nurse plants may be considered to restore “dehesas” instead of expensive seedling irrigation techniques. Several studies have promoted abandoning grazing to increase holm oak self-regeneration in “dehesas”. However, creating closed patches of naturally occurring evergreen shrubs could provide suitable sites for oak planting when necessary, thus enhancing seedling recruitment without damaging the environmental and economic value of these ecosystems.

Keywords Nurse plant · Photosynthetically active radiation · Seedling emergence timing · Seedling longevity · Summer drip-irrigation of seedlings

1 Introduction

Many oak species have difficulty in regenerating from seedlings in different areas of the world (e.g., Crow 1988; Keeley 1992; Asbjornsen et al. 2004; Brudvig and Asbjornsen 2008). In the Mediterranean and other seasonally dry environments recruitment of new oaks is frequently hindered by severe drought, which causes high early seedling mortality (e.g., Di Castri et al. 1981; Herrera et al. 1994; Pausas et al. 2004; Badano et al. 2009; Rodríguez-Calcerrada et al. 2010). Acorn predation, dispersal failure and lack of “safe sites” (sensu Harper 1977) for acorns and seedlings are additional limitations to the recruitment of new oaks (Crow 1988; Santos and Tellería 1997; Siscart et al. 1999; Leiva and Fernández-Alés 2003; Pulido and Díaz 2005). *Quercus ilex* subsp. *ballota* L. holm-oak—a broadly

Handling Editor: Douglass Jacobs

Contribution of the co-authors M.J.L. designed the experiment, wrote the paper and conducted data analysis. J. M.M.-L. designed the experiment, and conducted data analysis. A. M.-V. designed the experiment, conducted data analysis, supervised the work and coordinated the research project.

M. J. Leiva · J. M. Mancilla-Leyton · Á. Martín-Vicente (✉)
Departamento de Biología Vegetal y Ecología,
Universidad de Sevilla,
Apartado de Correos 1095,
41080 Seville, Spain
e-mail: angelm@us.es

extended species in the Mediterranean area of the Iberian Peninsula—also experiences the aforementioned recruitment limitation (Pulido and Díaz 2005; Siscart et al. 1999). In this region the species forms a genuine, human-derived, savanna-like ecosystem type, named locally “dehesa” in Spain, and “montado” in Portugal (San-Miguel 1994; Blanco et al. 1997; Costa et al. 2006).

The Spanish “dehesas” derive from a long history of human transformation of Mediterranean forest through clearing, browsing and grazing, although they have expanded considerably over the past two centuries (Costa et al. 2006; Martín-Vicente and Fernández-Alés 2006). Today they occupy over 3 million ha and are devoted to extensive livestock grazing and wild game. The “dehesas” are composed of an overstorey of scattered oaks (mainly holm-oak and secondary *Q. suber* L. cork oak), at 20–30 trees/ha, and an annual grasslands layer. Shrubs interspersed in the grassland matrix may also occur but they are usually confined to less transformed and intensively grazed patches, usually dedicated to wild game. Mediterranean “dehesas” are considered a model of sustainable resource-use to all fragile areas in the Mediterranean region (Joffre et al. 1988). They are of high environmental value because they support high animal and plant biodiversity and provide important environmental services such as supplying high quality food products, regulating water and carbon cycles and preventing the spread of wild fires (Doctor-Cabrera 2003; Costa et al. 2006). For those reasons “dehesas” are to be preserved under the EU Habitats Directive, and part of their territory has been included as a Biosphere reserve by UNESCO’s MaB programme (“Dehesas de Sierra Morena”).

Holm-oak is undergoing a severe decline process at present in many Spanish “dehesas” due to pathogens, former inappropriate soil management, and/or climate change (Brasier et al. 1993; Barberó et al. 1992; Peñuelas et al. 2001; Moreira and Martins 2005). This situation, and the aforementioned low recruitment of new individuals to the populations, threatens the long term persistence of “dehesas” (Pulido et al. 2001; Moreno and Pulido 2009). For this reason it is important to develop proper methods to improve recruitment of new seedlings in “dehesas”.

The common strategy of mass planting tree seedlings in open spaces is inadequate to restore “dehesas” or deforested areas in Mediterranean and seasonally dry environments because of high seedling mortality during summer (e.g., Gómez-Aparicio et al. 2004; Leiva and Fernández-Alés 2005; Castro and Frietas 2009). Planting holm-oak acorns or seedlings in open spaces and irrigating them during the first summer is another technique that has been used to afforest abandoned agriculture lands (e.g., Gimeno et al. 1994; Rey-Benayas 1998). In addition, the use of shrubs as nurse plants for woody seedlings has been applied successfully to the restoration of degraded Mediterranean areas

using different species (see, for instance, Gómez-Aparicio et al. 2004; Padilla and Pugnaire 2006; Rey et al. 2009). In this case, seedlings of the target species are planted beneath a shrub canopy, which ameliorates the microclimate during summer, causing a decrease in seedling mortality (e.g., Maestre et al. 2001; Castro et al. 2004, 2006; Gómez-Aparicio et al. 2004; Rey et al. 2009). The use of this technique is based on the hypothesis that, under stressful conditions, the negative effect of competition between plants is compensated by protection against environmental stress, resulting in net facilitation (Bertness and Callaway 1994; Callaway et al. 1997). However the nurse-based technique has shown to be insufficient to restore degraded oak forests in seasonally dry tropical environments (Asbjørnsen et al. 2004) where a combination of both methods, i.e., seedling irrigation during first summer and shrubs used as nurse plants, was necessary to reach adequate levels of seedling survival (Badano et al. 2009). Despite the importance of ensuring holm-oak regeneration in the Mediterranean “dehesas”, no studies have been carried out in this area on different methods to improve seedling recruitment.

This paper analyses the efficacy of: (1) shrubs used as nurse plants, (2) summer drip irrigation of seedlings, and (3) both methods combined to restore a “dehesa” in a mid-mountain Mediterranean area in southern Spain. *Myrtus communis* L.—an evergreen Mediterranean shrub abundant in slightly grazed “dehesa” patches—was used as nurse plant for holm-oak seedlings.

2 Methods

The study was conducted in a representative “dehesa” stand located in the “Sierra Norte de Sevilla” Natural Park (37°40' N, 5°59'W), southern Spain. Climate in the area is Mediterranean with 600–950 mm mean annual rainfall and 17.6–13.4 °C mean annual temperature (IMA 2006). Rain falls mainly between mid-September and mid-May and is negligible during the summer in an average year. The stand is at 400 m a.s.l. mean altitude, on a flat area. The soil is slightly acid, derived from granite rock and its depth is ca 60 cm. The holm-oak mean density is 20 individuals/ha. The understorey consist of annual grasslands and interspersed shrubs, of which myrtle is the major species, forming scattered patches of 7–9 m² canopy cover and 1.3–1.8 m canopy height. The site is used for game of red deer *Cervus elaphus* L. and wild boar *Sus scrofa* L.

A field experiment was carried out to compare different methods for holm-oak seedling recruitment. Four treatments, namely, myrtle irrigated (MI), myrtle rainfed (MR), open irrigated (OI) and open rainfed (OR) were considered with five replicates, Myrtle and open patches (i.e., full-sun)

were selected with a minimal distance of 4 m between a myrtle plant and an open patch. Each treatment was applied on an elementary 2.5×3 m patch beneath the myrtle canopy (MI, MR) or in full-sun (OI, OR). The irrigated plots received a summer drip irrigation and the others were just rainfed.

The drip irrigation system was installed at the beginning of the experiment (i.e., January 2006). It consisted of five, 1,000 L IBC SLX 1400 tanks that were connected to 16 mm T-tape drip irrigation tapes (33 cm emitter spacing) by polyethylene pipes (32 mm ϕ and 6 ATM, AGR), polyethylene ELBOWS 90° (32 mm ϕ), polyethylene tee connectors (32 mm ϕ) and polyethylene ball valves (PN 25 1") and received water from an irrigation reservoir using a vehicle mounted pump.

Acorns were sown in plots at 0.5×0.33 m spacing (i.e., 40 acorns/plot; 800 acorns in total) in early January. They were buried 5 cm deep into the soil and were protected individually with open top, wire mesh cylinders (8 cm diameter $\times$ 40 cm high) that were partially buried into the soil to avoid rodent predators. Each protector was tagged with a code for subsequent tracking of seedlings. A mechanical auger (Stihl BT 45) was used to make sowing holes (10 cm in diameter $\times$ 8 cm in depth). The acorns used in this experiment were collected previously in the stand, all from the same holm-oak tree to avoid maternal differences. They were stored for a month in a cold chamber at 4 °C and then selected for sound appearance (i.e., non-external damage) and homogeneous size (i.e., 3 cm in length) before sowing.

Irrigation treatment began in late spring and consisted of supplying 50 L water/seedling in four events: late May, mid-June, mid-July and mid-August (i.e., 12.5 L/seedling/event). Field records on seedling state (i.e., emerged, non-emerged, alive, dead) were recorded every 2 weeks during the 1st study year (2006) and monthly during the 2nd study year (2007). An additional record of seedling survival was carried out at the end of the 3rd year (2008). Seedling height was measured in the set of seedlings that were still alive at the end of each year. When the experiment ended, shoots and roots of 20 randomly selected seedlings, each from a different plot, were harvested, oven-dried (80 °C for 48 h) and weighed in the laboratory. Roots were excavated to 40 cm in depth.

Abiotic conditions were characterized during the 1st experimental year. Air temperature was recorded at 30 min frequency using eight data loggers (HOBO H8 Pro Series) placed in randomly selected plots (i.e., four open and four myrtle plots) 10 cm aboveground. Photosynthetically active radiation (PAR) was measured monthly using a 1-m long line quantum sensor (LI 191 Line Quantum Sensor) that was punctually placed in each plot. Measurements were taken at noon on clear days. Data on monthly rainfall during the study years were provided by a meteorological station close

to the stand (C.H.G, station 732, Spanish Environmental Office).

2.1 Data treatment

Differences among treatments in number of emerged seedlings per plot were analyzed using Kruskal-Wallis test and the same test was used to analyze differences among treatments in number of living seedlings per plot in the 3rd year of the experiment. Duncan tests on the entire set of observations ranked from the smallest to the largest were performed to detect homogeneous groups of treatments (Conover and Iman 1981). Survival analysis (Kaplan-Meier method and log-rank test) were used to examine differences among treatments in emergence timing (i.e., time from sowing to seedling emergence) and in seedling longevity (i.e., time from seedling emergence to death). Living seedlings at the end of experimental period were managed as censored data in these analyses (Swinscow and Campbell 2002). Treatment effect on seedling height was tested using one-way ANOVA. Data on seedling biomass were analyzed using General Linear Models with habitat type (i.e., open, myrtle) and watering treatment (i.e., rainfed, irrigated) treated as random and fixed effects, respectively. Differences among treatments in air temperature were analyzed using *T*-test for paired comparisons (Sokal and Rohlf 1981). All analyses were carried out using SPSS Statistic 17.0 software (SPSS, Chicago, IL).

3 Results

3.1 Abiotic conditions during the experimental period

The total annual rainfall during the experimental period—years 2005/2006, 2006/2007 and 2007/2008—was 627, 995 and 787 mm respectively (Fig. 1). Those values were considered to fall within the average annual rainfall in the area (i.e., 600–950 mm) except for the year 2007, which was slightly wetter especially during autumn. Air temperatures measured during the 1st experimental year (Table 1) differed significantly in the myrtle and open microhabitats ($P=0.001$, 0.002 and 0.002 for maximal, mean and minimal air temperatures, respectively). The former exhibited lower mean and maximal air temperatures but higher minimal temperature than the latter. Maximal air temperature exhibited the greatest difference among the microhabitats tested. On average it was 4.3 °C lower beneath the myrtle canopy than in full sun. There were also significant ($gl=11$, $t=10.59$, $P<0.001$) differences with regard to microhabitats in photosynthetically active radiation (PAR) reaching the understory. PAR was ca 20-fold lower beneath the dense myrtle canopy (Table 1) than in full sun.

Fig. 1 Monthly rainfall during the study period

3.2 Seedling emergence

A total 473 seedlings (i.e., 59 % sown acorns) emerged throughout the whole experiment, all of them during the 1st experimental year. The mean number of emerged seedlings per plot did not change significantly among treatments

($\chi^2=7.046$; $gl=3$; $P=0.07$) although it was slightly higher in MI than in the other treatments (Table 2). The time span from acorn sowing to seedling emergence (i.e., emergence timing) ranged from 113 to 333 days. Most seedlings (i.e., 96 %) emerged before summer but some of them (4 % seedlings) emerged in autumn.

Table 1 Monthly air temperature and photosynthetically active radiation (PAR) through 2006 (mean $\pm$ SE)

	Air temperature (°C)			PAR (μmol m ⁻² s ⁻¹)
	Minimum	Mean	Maximum	
Open				
January	−0.9±0.4	5.3±0.3	15.2±0.5	957±17
February	−1.0±0.5	6.3±0.3	17.3±0.9	1,135±9
March	3.6±0.3	10.9±0.3	20.4±0.4	1,341±14
April	7.8±0.5	14.9±0.5	24.9±0.9	1,437±14
May	10.1±0.3	20.5±0.4	34.6±0.4	1,758±29
June	11.4±0.3	24.8±0.4	41.4±0.9	1,953±29
July	12.8±0.3	28.0±0.6	47.0±0.6	2,031±56
August	13.2±0.4	27.0±0.8	44.5±0.9	1,749±57
September	11.7±0.4	21.5±0.4	37.8±0.5	1,583±20
October	10.5±0.4	17.2±0.5	28.1±0.9	938±17
November	7.2±0.3	12.1±0.3	21.6±0.4	809±18
December	0.9±0.5	6.5±0.6	16.3±0.8	784±18
Myrtle				
January	0.7±0.3	5.5±0.3	11.7±0.5	56±16
February	0.5±0.5	6.2±0.4	13.9±0.8	65±14
March	4.2±0.3	10.2±0.3	18.5±0.4	78±20
April	7.4±0.5	14.1±0.4	23.1±0.8	83±20
May	9.7±0.3	18.0±0.3	29.1±0.5	101±37
June	12.3±0.3	21.8±0.5	34.7±0.8	112±41
July	14.3±0.3	26.0±0.4	41.3±0.6	117±51
August	14.7±0.4	25.4±0.5	38.7±0.9	101±61
September	13.2±0.4	20.4±0.4	32.2±0.4	91±41
October	11.9±0.4	16.8±0.7	24.1±0.7	55±22
November	8.7±0.3	11.9±0.6	17.4±0.4	47±26
December	2.3±0.5	6.8±0.7	13.5±0.8	48±21

Table 2 Seedling emergence timing (mean $\pm$ SE and median values resulting from log rank test are shown) and number of emerged seedlings under different treatments (mean $\pm$ SE values and averaged ranks according to Kruskal–Wallis test are shown)

Treatment	Emergence timing (days)		Emergence number (seedlings/plot)	
	Mean	Median	Mean	Average rank
Open rainfed	121 $\pm$ 1.1	113	22.6 $\pm$ 0.2	9.8
Open irrigated	122 $\pm$ 1.2	113	22.8 $\pm$ 1.8	10.4
Myrtle rainfed	126 $\pm$ 1.5	130	21.2 $\pm$ 1.2	6.0
Myrtle irrigated	130 $\pm$ 1.2	130	26.4 $\pm$ 1.2	15.8

To analyze differences among treatments in seedling emergence timing, log rank tests were first conducted to compare emergence timing among replicated plots within each treatment. As the results indicated no significant differences among plots ($X^2=1.961$, $P=0.16$; $X^2=0.005$, $P=0.95$; $X^2=0.042$, $P=0.34$ and $X^2=1.084$, $P=0.29$ for OR, OI, MR and MI treatments, respectively) data were pooled from replicated plots to subsequent comparisons among treatments. The emergence timing of seedlings (Table 2) exhibited general significant differences among treatments ($X^2=19.23$, $gl=3$, $P=0.0001$). Seedlings emerged significantly faster in open microhabitat (OR and OI treatments) than in myrtle (MR and MI treatments).

3.3 Seedling longevity and survival

To analyze differences among treatments in seedling longevity, survival analyses were carried out. As in previous cases, data from replicated plots within each treatment were pooled as there were no significant differences among replicated plots within any treatment (log rank tests: $X^2=5.87$, $P=0.21$; $X^2=3.56$, $P=0.47$; $X^2=8.41$, $P=0.78$ and $X^2=6.85$, $P=0.14$ for OR, OI, MR and MI treatments, respectively).

Survival functions (Fig. 2) and log rank test (Table 3) indicated general significant ($X^2=71.14$; $P<0.001$) differences among treatments in seedling longevity. Median seedling longevity was significantly longer beneath the myrtle canopy (MR and MI treatments) than in full sun (OR and OI

treatments). The irrigation treatment had no significant effect on seedling longevity beneath the myrtle canopy (i.e., MR vs MI treatments) but it slightly increased seedling longevity in full sun (i.e., OR vs OI treatments). At the end of the experiment (i.e., December 2008) general differences among treatments were still highly significant ($X^2=10.764$; $gl=3$; $P=0.013$) although irrigation treatment had no significant effect on seedling survival in full sun (i.e., OR vs OI treatment) nor beneath the Myrtle canopy (i.e., MR vs MI treatment).

3.4 Seedling height and biomass

Seedling height varied significantly among treatments at the end of the 1st and 2nd study years ($P=0.01$ and 0.045 for years 2006 and 2007, respectively; Fig. 3) with the shortest seedlings in the OR treatment. The same pattern was observed at the end of the 3rd study year (i.e., 2008) although differences among treatments were not significant ($P=0.061$) in this case.

The biomass components of seedlings and their allocation to roots and shoots at the end of experiment changed significantly among treatments (Table 4) due to a significant effect of microhabitat type (i.e., open, myrtle). Irrigation treatment and interaction among irrigation and microhabitat types had no significant effect on those variables. Seedlings grown in full sun were heaviest and allocated more biomass to their roots than seedlings grown beneath the myrtle canopy (Fig. 4).

Fig. 2 Survival curves of holm-oak seedlings in different treatments: OR open rainfed, OI open irrigated, MR myrtle rainfed, MI myrtle irrigated

4 Discussion

A decrease in air temperature found beneath the Myrtle canopy (Table 1) is a common micro environmental change induced by shrubs and tall plants. Its effect on seedling survival has been studied repeatedly in seasonally dry environments (Maestre et al. 2003; Breshears et al. 1998; Gomez-Aparicio et al. 2005). However, its effect on seedling emergence, assessed in this study, has been analyzed less frequently. The results of this study indicated significantly faster emergence when acorns were sown in full sun (Table 2) where the temperature was higher (Table 1). The

Table 3 Paired comparisons (log rank tests) among treatments for seedling emergence timing and seedling longevity. *OR* open rainfed, *OI* open irrigated, *MR* myrtle rainfed, *MI* myrtle irrigated

		OI	MR	MI
Emergence	OR	$\chi^2=0.60$, $P=0.439$	$\chi^2=8.59$, $P<0.003$	$\chi^2=28.77$, $P<0.001$
	OI	–	$\chi^2=4.97$, $P=0.026$	$\chi^2=21.01$, $P=0.001$
	MR	–	–	$\chi^2=4.33$, $P=0.067$
Survival	OR	$\chi^2=11.2$, $P=0.001$	$\chi^2=38.5$, $P<0.001$	$\chi^2=47.9$, $P<0.001$
	OI	–	$\chi^2=19.5$, $P<0.001$	$\chi^2=16.9$, $P<0.001$
	MR	–	–	$\chi^2=0.23$, $P=0.633$

close connection between germination timing and temperature requirements for germination exhibited by most seeds (Harper 1977; Fenner and Thompson 2005) likely explain the reduction in emergence timing of holm-oak seedlings under warmer full sun conditions. A positive correlation between the establishment of tree seedlings and spring temperature over a sequence of years, alternating warm and cold springs has been also found in temperate forests (Ibáñez et al. 2007). However, belowground competition by Myrtle during holm-oak seedling pre-emergence could have also played a role as this is common in different kind of habitats, including arid and semiarid areas (see Fowler 1986 for a review; Casper and Jackson 1997).

The low longevity and survival of non irrigated holm-oak seedlings grown in full sun in spite of normal-to-high annual rainfall (i.e., 627, 995 and 787 mm) during our study years is a general pattern for many woody species in Mediterranean environments (e.g., Di Castri et al. 1981; Herrera et al. 1994; Pausas et al. 2004; Badano et al. 2009; Rodríguez-Calcerrada et al. 2010). In fact holm-oak seedlings are found to exhibit high drought intolerance when compared to other Mediterranean species (Zavala et al. 2000; Sánchez-Gómez et al. 2006). Under exposed full sun conditions, summer irrigation increased seedling longevity greatly during the 1st experimental year (Fig. 2), but this beneficial effect was much lower during the 2nd experimental year, and was completely lost at the end of the experiment. Those results disagree with studies carried out in Mediterranean set-aside agriculture lands (Rey-Benayas 1998) where 1st year summer irrigated *Quercus ilex*

seedlings exhibited a high survival rate from 1st to last (i.e., 3rd) experimental year. However soil properties in these abandoned agricultural environments undoubtedly differ from those of the never-ploughed, highly trampled soils in our study sites. It has been stated that the first growing season dry period is the main bottle-neck for woody seedling recruitment in seasonally dry environments (e.g., Herrera et al. 1994; Rey-Benayas 1998; Rey and Alcántara 2000; Pulido and Díaz 2005). This may explain why the analysis of irrigation effect on seedling survival is limited to the 1st experimental year in some studies (Badano et al. 2009). However, the results of the present study do not endorse those assumptions as they show the relevance of a longer period. It is important to note that seedling survival in full sun at the end of the experiment was low regardless of whether they were irrigated or not during establishment in summer. However, in wetter Mediterranean mountain areas enhanced *Q. ilex* seedling survival by irrigation in open areas has been found (Mendoza et al. 2009).

By contrast, the high and temporally consistent facilitative effect of myrtle on holm-oak seedlings recruitment (Fig. 2) agrees with a commonly observed positive nurse effect of shrubs and tall plants on recruitment of woody seedlings in Mediterranean and other seasonally dry environments (for instance Maestre et al. 2001; Castro et al. 2002, 2004, 2006; Gómez-Aparicio et al. 2004; Marañón et al. 2004; Rey et al. 2009). Changes in micro environmental conditions involved in the aforementioned nurse effect include protecting seedlings against high irradiance and temperature, increasing humidity, which improves seedling

Fig. 3 Seedling height at the end of each study year (mean + SE). Similar letters indicate non significant differences according to HDS Tukey tests

Table 4 *P*-values for the model and variation sources for seedling biomass components and their allocation to roots and shoots

	Model	Micro habitat type	Watering treatment	Interactions
Total	<0.00	0.01	0.25	0.08
Shoot	<0.00	0.04	0.48	0.12
Root	<0.00	0.00	0.07	0.05
Root/shoot	<0.00	0.00	0.06	0.18

water status, and increasing nutrient availability in rhizosphere by high litter accumulation and decomposition (for instance Callaway 1995; Canham et al. 1996; Castro et al. 2002 and references therein). Our results on a lack of significant effect of 1st year summer irrigation in the Myrtle microhabitat (Tables 1, 2; Fig. 2) suggest that holm-oak seedlings apparently did not experience a high water constraint beneath the dense myrtle canopy. Those results agree with findings on shaded Mediterranean woodlands where summer irrigation had no effect on *Q. ilex* seedling survival (Mendoza et al. 2009), and with studies on the low impact of drought on woody seedling survival, growth and physiological and structural leaf response under shade conditions in Mediterranean environments (Sack 2004; Quero et al. 2006; Sánchez-Gómez et al. 2006).

However, these findings disagree with studies carried out in seasonally dry tropical environments (Badano et al. 2009), where a combination of both techniques, i.e., planting oak seedlings beneath canopy of pioneer shrubs and irrigating them during the dry season, was necessary to reach restoration goals. Canopy characteristics of species used as nurse plants is likely to be an important determinant of their facilitative effect on recruitment of target seedlings. The differential effect on recruitment of target woody seedlings of several shrub species used as potential nurse plants was found in degraded mountainous Mediterranean areas (Gomez-Aparicio et al. 2005). The species used in this experiment, *Myrtus communis*, is an evergreen sclerophyllous shrub (Valdés et al. 1987) whose closed canopy intercepts a high level of sun radiation as evidenced by the low PAR level reaching its understorey (i.e., 6 % full-light PAR on average) in our study stand. A similarly low (i.e., 3–33 %)

irradiance level has been also found in other Mediterranean forest understorey (Marañón et al. 2004; Valladares et al. 2008), and has been used as representative light-end in controlled experimental studies on Mediterranean woody species (Broncano et al. 1998; Quero et al. 2006; Sánchez-Gómez et al. 2006). Holm-oak has been defined as a shade-tolerant, slow-growing species whose seedlings are able to survive deep shade conditions (Espelta et al. 1995; Zavala et al. 2000)—a pattern exhibited by other big-seeded Mediterranean woody species such as holm-oak (Sánchez-Gómez et al. 2006). Thus deep shade generated by myrtle canopy and associated environmental changes provide holm-oak seedlings with suitable conditions for recruitment.

Our results on seedling biomass and height under different micro environmental conditions indicate a high and significant impact of PAR reduction on seedling growth, as all biomass components were significantly lower in seedlings growing beneath the myrtle canopy than in the few that survived in full sun (Table 3, Fig. 3). These results agree with studies in controlled conditions reporting that *Q. ilex* seedlings growing at low (i.e., 1–16 %) PAR level exhibited poor biomass growth by comparison to seedlings growing at high (i.e., 36–100 %) PAR level (Retana et al. 1999, Sánchez-Gómez et al. 2006). The relatively lower allocation of biomass to roots and higher to shoots of seedlings growing beneath Myrtle canopy in comparison to full sun conditions (Fig. 4) is a common response of many woody seedlings to light shortage (Reich et al. 1998). Seedlings growing beneath Myrtle canopy tended to be taller than those growing in full-sun (Fig. 3). However, only the OR treatment differed significantly from the others during the 1st experimental year, while differences were lost afterwards. An

Fig. 4 Biomass components of seedlings and their allocation to roots and shoots at the end of experiment in two microhabitats. Mean values (+ SE). Open bars Open space, black bars beneath myrtle canopy

increase in seedling height in low-light environments by comparison to high-light ones is usually related to elongation (Valladares et al. 2002)—a well documented shade avoidance strategy in plants (Pearcy et al. 2005).

4.1 Management implications

In view of the low efficiency of 1st year summer irrigation—an expensive treatment that did not increase the low general recruitment of holm-oak seedlings in open spaces nor improve the already high seedling recruitment beneath myrtle in our study stand—this technique cannot be considered as a general solution to restore Mediterranean “dehesa” ecosystems. By contrast, the use of *Myrtus communis* and other naturally occurring evergreen shrubs (e.g., *Arbutus unedo* L., *Pistacia lentiscus* L. etc.), which provide deep shade beneath their canopies, as nurse plants should be taken into account in planning restoration of such ecosystems. The patchy distribution of myrtle and other evergreen species and/or their absence in some “dehesas” made extensive use of this technique difficult. To enhance regeneration of holm-oak in “dehesa”, passive restoration, i.e., abandonment of grazing activity over 20 years that led to shrub encroachment and an associated increase in holm-oak saplings and juveniles (Ramírez and Díaz 2008), was proposed. However, long-abandoned “dehesas” usually become dominated by summer semideciduous rockroses like *Cistus ladanifer* and other pioneer shrubs (Castro and Freitas 2009) that do not provide deep shade. Their effect on holm-oak seedling recruitment is still controversial (Gómez-Aparicio et al. 2004; Moreno-Marcos et al. 2009). In addition, abandoned “dehesas” lose their value as grazing systems.

An alternative solution is to create closed patches in “dehesas” by active restoration, i.e., planting evergreen shrubs when necessary. That would provide the proper conditions for the sexual regeneration of holm-oak as it is a shade-tolerant species during the regenerative stage (Espelta et al. 1995; Zavala et al. 2000). Moreover, such patches, which should include meaningful assemblages of Mediterranean shrubs, would provide shelter and food resources for animals, including acorns dispersers (Pulido and Díaz 2005), thus increasing general plant and animal biodiversity in these systems. A careful design of patch composition, size and distribution would provide suitable sites for planting holm-oak seedlings or acorns without damaging the environmental and economic values of “dehesas” ecosystems.

Acknowledgements The authors wish to thank Juan Carlos Costa and “Las Navas-Berrocal” staff for logistic support and field facilities. We also thank Esteban Serrano for field and laboratory assistance. Special thanks to Rocío Fernández-Alés for useful comments on early version of this manuscript. Comments of two anonymous reviewers have improved this work. Rafael Portillo checked the English of this paper. This study was funded by the “Empresa de Gestión Medioambiental” S.A. (OG-039/04)

References

- Asbjornsen H, Vogt AK, Ashton MS (2004) Synergistic responses of oak, pine and shrub seedlings to edge environments and drought in a fragmented tropical highland oak forest, Oxaca, Mexico. *For Ecol Manag* 192:313–344
- Badano EI, Pérez D, Vergada CH (2009) Love of nurse plants is not enough for restoring Oak forests in a seasonally Dry tropical environment. *Restor Ecol* 17:571–576
- Barberó M, Loisel R, Quézel P (1992) Biogeography, ecology and history of Mediterranean *Quercus ilex* ecosystems. *Vegetatio* 99–100:19–34
- Bertness MD, Callaway RM (1994) Positive interactions in communities. *Trends Ecol Evol* 5:191–193
- Blanco E, Casado MA, Costa M, Escribano R, García M, Génova M, Gómez A, Gómez F, Moreno JC, Morla C, Regato P, Sáinz H (1997) Los Bosques Ibéricos. Una interpretación Geobotánica. Planeta, Madrid
- Brasier CM, Robredo F, Feraz JFP (1993) Evidence for *Phytophthora cinnamomi* involvement in Iberian oak decline. *Plant Pathol* 42:140–145
- Breshears DD, Nyhan JW, Heil CE, Wilcox BP (1998) Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *Int J Plant Sci* 159:1010–1017
- Broncano MJ, Riba M, Retana J (1998) Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex*) and Aleppo pine (*Pinus halepensis*): a multifactor experimental approach. *Plant Ecol* 1:17–26
- Brudvig LA, Asbjornsen H (2008) Patterns of oak regeneration in a Midwestern savanna restoration experiment. *For Ecol Manag* 255:3019–3025
- Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349
- Callaway RM, Walker LR, Abrams PA (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965
- Canham CD, Berkowitz AR, Kelly VR, Lovett GM, Ollinger SV, Schnurr J (1996) Biomass allocation and multiple resource limitation in tree seedlings. *Can J For Res* 26:1521–1530
- Casper BB, Jackson RB (1997) Plant competition underground. *Annu Rev Ecol Syst* 28:545–570
- Castro H, Freitas H (2009) Above-ground biomass and productivity in the Montado: from herbaceous to shrub dominated communities. *J Arid Environ* 73:506–511
- Castro J, Zamora R, Hódar JA, Gómez JM (2002) Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. *Restor Ecol* 10:297–305
- Castro J, Zamora R, Hódar JA, Gómez JM, Gómez-Aparicio L (2004) Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restor Ecol* 12:352–358
- Castro J, Zamora R, Hódar JA (2006) Restoring *Quercus pyrenaica* forests using pioneer shrubs as nurse plants. *Appl Veg Sci* 9:137–142
- Conover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *Am Stat* 35:124–129
- Costa JC, Martín-Vicente A, Fernández-Alés R, Estirado-Oliet M (2006) Dehesas de Andalucía Caracterización Ambiental. Consejería de Medio Ambiente—Junta de Andalucía, Sevilla
- Crow TR (1988) Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. *For Sci* 34:19–40
- Di Castri F, Goodall DW, Specht RL (1981) Mediterranean-type shrublands. Elsevier, Amsterdam
- Doctor-Cabrera AM (2003) Territorio e incendios forestales. Consejería de Medio Ambiente—Junta de Andalucía, Sevilla
- Espelta JM, Riba M, Retana J (1995) Pattern of seedling recruitment in west Mediterranean coppiced holm-oak (*Quercus ilex* L.) Mediterranean forest as influenced by canopy development. *J Veg Sci* 6:465–472

- Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge, RU, pp 250
- Fowler N (1986) The role of competition in plant communities in arid and semiarid regions. *Annu Rev Ecol Syst* 17:89–110
- Gimeno A, Hernández AJ, Pastor J, Rey-Benayas JM, Sánchez Y (1994) Técnicas de cultivo para reforestar con encinas. *Quercus* 105:31–33
- Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol Appl* 14:1128–1138
- Gomez-Aparicio L, Valladares F, Zamora R, Quero JL (2005) Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. *Ecography* 28:757–768
- Harper JL (1977) Population biology of plants. Academic, London
- Herrera CM, Jordano P, López-Soria L, Amat JA (1994) Recruitment of a mast-fruited, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol Monogr* 64:315–344
- Ibáñez I, Clark JS, Shannon L, Lambers JHR (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecol Monogr* 77:163–177
- IMA (2006) Medio Ambiente en Andalucía. Informe. Junta de Andalucía, Sevilla
- Joffre R, Vacher JDe, los Llanos C, Long G (1988) The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference of the Sierra Morena area of Spain. *Agrofor Syst* 6:71–96
- Keeley JE (1992) Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology* 73:1194–1208
- Leiva MJ, Fernández-Alés R (2003) Post-dispersive losses of acorns from Mediterranean savanna-like forests and shrublands. *For Ecol Manag* 176:265–271
- Leiva MJ, Fernández-Alés R (2005) Factors limiting the sexual regeneration of holm-oak *Quercus ilex* subsp. *ballota* in dehesa agroforestry ecosystems of Sierra Morena Spain. *Adv Geoeol* 37:263–271
- Maestre FT, Bautista S, Cortina J, Bellot J (2001) Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecol Appl* 11:1641–1655
- Maestre FT, Bautista S, Cortina J (2003) Positive, negative and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84:3186–3197
- Marañón T, Zamora R, Villar R, Zavala MA, Quero JL, Pérez-Ramos I, Mendoza I, Castro J (2004) Regeneration of tree species and restoration under contrasted Mediterranean habitats: field and glasshouse experiments. *Int J Ecol Environ Sci* 30:187–196
- Martín-Vicente A, Fernández-Alés R (2006) Long term persistence of dehesas. Evidences from history. *Agrofor Syst* 67:19–28
- Mendoza I, Zamora R, Castro J (2009) A seeding experiment for testing tree-community recruitment under variable environments: Implications for forest regeneration and conservation in Mediterranean habitats. *Biol Conserv* 142:1491–1499
- Moreira AC, Martins JMS (2005) Influence of site factors on the impact of *Phytophthora cinnamomi* in cork oak stands in Portugal. *For Pathol* 35:145–162
- Moreno G, Pulido F (2009) The functioning, management, and persistence of Dehesas. Agroforestry in Europe. In: Rigueiro-Rodríguez A, McAdam J, Mosquera-Losada MR (eds) Advances in agroforestry, vol 6. Springer, Berlin, pp 127–160
- Moreno-Marcos G, Rolo-Romero V, López-Díaz L (2009) Consecuencias de la matorralización de la dehesa para la regeneración natural de la encina (eds. SECF-Junta de Castilla y León)
- Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. *Front Ecol Environ* 4:196–202
- Pausas JG, Bladé C, Valdecantos A, Seva JP, Fuentes D, Alloza JA, Vilagrosa A, Bautista S, Cortina J, 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
- Pearcy RW, Muraoka H, Valladares F (2005) Crown architecture in sun and shade environments: assessing function and tradeoffs with a 3-D simulation model. *New Phytol* 166:791–800
- Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora. *For Sci* 47:214–218
- Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole cycle approach. *EcoScience* 12:92–102
- Pulido FJ, Díaz M, Hidalgo SJ (2001) Size-structure and regeneration of holm-oak (*Quercus ilex*) forests and dehesas: effects of agroforestry use on their long-term sustainability. *For Ecol Manag* 146:1–13
- Quero JL, Villar R, Marañón T, Zamora R (2006) Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytol* 170:819–834
- Ramírez JA, Díaz M (2008) The role of temporal shrub encroachment for the maintenance of Spanish holm oak *Quercus ilex* dehesas. *For Ecol Manag* 255:1976–1983
- Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C (1998) Close association of RGR, leaf and root morphology, seeds mass and shade tolerance in seedling of nine boreal tree species growing in high and low light. *Funct Ecol* 12:337–338
- Retana J, Espelta JM, Gracia M, Riba M (1999) Seedling recruitment. In: Rodá F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean evergreen oak forests. Ecological studies, vol 137, Springer, Berlin, pp 89–101
- Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europea*): connecting patterns of seed dispersal to seedling establishment. *J Ecol* 88:622–633
- Rey PJ, Siles G, Alcántara JM (2009) Community-level restoration profiles in Mediterranean vegetation: nurse-based vs. traditional reforestation. *J Appl Ecol* 46:937–945
- Rey-Benayas JM (1998) Growth and mortality in *Quercus ilex* L. seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural lands. *Ann Sci For* 55:801–807
- Rodríguez-Calcerrada J, Cano FJ, Valbuena-Carabaña M, Gil L, Aranda I (2010) Functional performance of oak seedlings naturally regenerated across microhabitats of distinct overstorey canopy closure. *New For* 39:245–259
- Sack L (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* 107:110–127
- Sánchez-Gómez D, Valladares F, Zavala MA (2006) Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytol* 170:795–806
- San-Miguel A (1994) La dehesa española. Origen, tipología, características y gestión. Fundación Conde del Valle de Salazar, Madrid
- Santos T, Tellería JL (1997) Vertebrate predation on holm-oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedlings recruitments. *For Ecol Manag* 98:181–187
- Siscart D, Diego V, Lloret F (1999) Acorn ecology. In: Rodá F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean evergreen oak forests. Ecological Studies, vol 137, Springer-Verlag, Berlin, pp 75–86
- Sokal RR, Rohlf FJ (1981) Biometry: the principles and practice of statistics in biological research. Freeman, New York
- Swinscow TDV, Campbell MJ (2002) Statistic at square one. BMJ Books, London
- Valdés B, Talavera S, Fernández-Galiano E (1987) Flora Vascular de Andalucía Occidental. Ketres, Barcelona

- Valladares F, Balaguer L, Martinez-Ferri E, Perez-Corona E, Manrique E (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytol* 156:457–467
- Valladares F, Zaragoza-Castel J, Sánchez-Gómez D, Matesanz S, Alonso B, Portsmuth A, Delgado A, Atkin OW (2008) Is shade beneficial for Mediterranean shrubs experiencing periods of extreme drought and late-winter frost? *Ann Bot* 102:923–933
- Zavala MA, Espelta JM, Retana J (2000) Constraints and trade-offs in Mediterranean plant communities: the case of holm-oak Aleppo pine forests. *Bot Rev* 66:120–140