

Irradiance and oak seedling survival and growth in a heterogeneous environment

Carolina Puerta-Piñero^{a,*}, José M. Gómez^a, Fernando Valladares^b

^aGrupo de Ecología Terrestre, Dpto. Ecología, Facultad de Ciencias, Universidad de Granada, Granada E-18071, Spain

^bInstituto de Recursos Naturales, Centro de Ciencias Medioambientales—CSIC, Serrano 115, Madrid E-28006, Spain

Received 6 July 2006; received in revised form 4 December 2006; accepted 21 January 2007

Abstract

The Mediterranean region emerges highly heterogeneous at every spatio-temporal scale. Key species shape a mosaic of patches (landscape units) composed of different microhabitats. Within these ecosystems irradiance appears as one of the most changing factors affecting communities' dynamic. However, the impact of irradiance on the species performance is still poorly known. In this study, we intended to explore whether irradiance heterogeneity influences early recruitment. We chose a patchy Mediterranean site. During 2001, 2002 and 2003 we marked naturally *Quercus ilex* emerged seedlings. We distinguished three landscape units (*Q. ilex* woodlands, shrublands and afforestations) and six microhabitats (oak, broom, tall shrub, subshrub, pine and open). For each seedling, we measured (1) irradiance as global site factor (GSF); (2) acorn presence; (3) acorn depth; (4) burial layer; (5) distance to the nearest co-specific adult. As estimates of seedling performance, we measured seedling survival and height. Estimates of seedling performance were higher in 2001 and 2002 than in 2003. Oak or pine microhabitats achieved higher survival rates than brooms or open areas whilst under oaks, brooms or in open areas seedling height was lower than under tall shrubs. Irradiance significantly affected seedling survival and growth. The lower the irradiance, the higher the survival. Maximal growth was found at intermediate irradiance, indicating that, in this system, moderate shade is crucial for *Q. ilex* seedling recruitment. Some microhabitats provide intermediate irradiance that combines positive effects on survival and growth. As a final point, dispersers' activity creates a heterogeneous distribution of acorn deposition filtering out part of the total irradiance present in the study site.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Light environment; Mediterranean region; *Quercus ilex*; Seedling performance; Spatial heterogeneity

1. Introduction

It is known that spatial heterogeneity in resource supply and abiotic conditions strongly controls individual performance in most species (Hutchings et al., 2000, 2003). Different interactions can influence population dynamics by directly altering their adjacent environment or indirectly varying the spatial patterns of plant recruitment (Callaway, 1995; Schupp and Fuentes, 1995; García et al., 2005; Gómez-Aparicio et al., 2005a,b). These effects occur mainly when diverse factors vary spatially, between microhabitats, habitats or even landscapes (Clark et al., 1998; Wiens, 2000). While heterogeneity can be provoked by biotic or abiotic causes, its consequences are often experienced by living organisms. Under these circumstances,

the spatial distribution of many plant species inhabiting heterogeneous landscapes can be a direct consequence of the availability of some key environmental factors (Watling and Press, 2000). Although spatial heterogeneity can act at any vital stages, its consequences are stronger on the first stages of life cycles (Gómez et al., 2003a). Seedlings represent one of the most vulnerable stages in the life cycle of most plant species, since they have not yet got enough size to face many negative ecological factors occurring in the environment (Silvertown and Charlesworth, 2001). Consequently, high mortality at this stage is extremely frequent in many plant species (Tripathi and Khan, 1990; Kitajima and Fenner, 2000; Gómez, 2004; Pulido and Díaz, 2005; Gómez-Aparicio et al., 2005a). Many recent studies have shown that early recruitment is particularly influenced by abiotic factors (Valladares, 2004; Gómez-Aparicio et al., 2004, 2005a).

Irradiance plays a crucial role in plant regeneration in many terrestrial ecosystems by influencing the recruitment and

* Corresponding author. Tel.: +34 958 246166; fax: +34 958 243238.
E-mail address: carol@ugr.es (C. Puerta-Piñero).

performance of many species (Pugnaire and Valladares, 1999; Beckage and Clark, 2003). This resource is particularly heterogeneous in space and time (Percy, 1999; Watling and Press, 2000). At the most basic level, spatial heterogeneity in irradiance creates variation in the available resources and hence in photosynthesis and growth (Percy, 1999). These consequences can result from alterations in different processes such as photosynthesis, water relations, pigment composition, biomass allocation, relative growth rate or survival (Turton and Duff, 1992; Gratani, 1997; Faria et al., 1998; Staudt and Bertin, 1998; Retana et al., 1999; Valladares et al., 2000; Watling and Press, 2000; Zavala et al., 2000; Oliveira and Peñuelas, 2002; Valladares, 2003; Gómez-Aparicio et al., 2005b). Due to the uneven distribution of irradiance in nature and the importance for plant recruitment and performance, light intensity is thereby a primary factor explaining the spatial heterogeneity of plant regeneration (Beckage and Clark, 2003). Despite the potentially high ecological relevance of irradiance in Mediterranean ecosystems, information on spatial and temporal heterogeneity on irradiance and its real role as an ecological factor is particularly scant (Gómez et al., 2004; Valladares and Guzmán, 2006). While irradiance can vary within and among spatial scales, in the temporal dimension this variability is superior at lower scales than at higher ones, i.e. irradiance varies most within the day or seasons than among years or decades (Valladares, 2003). At a regional scale, vegetation pattern is the main cause of variability in irradiance, whereas at a local scale heterogeneity in overstorey canopy structure is the principal factor (Caldwell and Percy, 1994; Watling and Press, 2000). Irradiance can be stressful for plant performance either when scarce or overabundant and thus, shows an “optimal response” at intermediate values (Pugnaire and Valladares, 1999; Valladares and Guzmán, 2006).

The main objective of this study is to assess the effect of irradiance heterogeneity on *Quercus ilex* L. early recruitment. Our working hypothesis is that irradiance has a detectable and significant signal on seedling performance in natural conditions. These consequences can be different for each estimate of performance (e.g. survival, growth) and could be detected regardless of different co-occurring and interacting factors (e.g. inter-annual variability, disperser activity). Specifically, we determined (i) to which extent irradiance availability in combination with biotic factors influence seedling survival and growth, and (ii) whether seedlings performance vary among landscape units, microhabitats and year of study.

2. Materials and methods

2.1. Study site and species

The study site is a 12-ha area at 1700 m a.s.l. within the Trevenque area, Sierra Nevada National Park (SE Spain, 37°5'N, 3°28'W). The landscape is a mosaic of small patches of *Q. ilex* woodlands coexisting with afforestation (*Pinus* spp.) stands. Within this landscape we can differentiate three main landscape units: (1) “oak woodlands”, fragments of *Q. ilex* woodlands intermingled with isolated pines and shrubs; (2)

“afforestations”, medium to large patches of pines; (3) “shrublands”, patches of different shrub species highly mixed together. For this study, six types of microhabitats (i.e. small internally-homogeneous patches) were considered: (1) “oak”, under the canopy of *Q. ilex*; (2) “pines”, mainly *Pinus sylvestris* Arnorld; (3) “tall shrubs”, under the canopy of shrub species >0.5 m tall, mostly composed of *Crataegus monogyna* Jacq., *Berberis vulgaris* L. and *Prunus ramburii* Boiss.; (4) “brooms”, beneath fabaceous tall shrubs, mostly *Cytisus reverchonii* (Degen and Hervier) Bean, *Genista cinerea* D.C. and *Genista versicolor* Boiss.; (5) “subshrubs”, under the canopy of stunted shrubs ≈30 cm high, mainly *Salvia lavandulifolia* Vahl., *Echinopartium boissieri* (Spach) Rothm., *Santolina canescens* Lag., *Thymus mastichina* L., and *Erinacea anthyllis* Link; (6) “open”, composed of bare soil with sparse short herbaceous cover. “Oak woodlands” and “shrublands” have representation of these six microhabitats, while “afforestation” has only the microhabitat “pine”. Table 1 shows between-microhabitat differences in major microclimatic and soil properties.

Holm-oak *Q. ilex* L. (Fagaceae) is a Mediterranean evergreen sclerophyllous species which presents masting years (Pulido and Díaz, 2005). It is distributed from SW France to N Morocco. In the Sierra Nevada high mountains, this oak species is found from 1000 to 1900 m a.s.l.. Acorns are dispersed in fall, both abiotically and biotically by jays and rodents (Gómez, 2003; Gómez et al., 2003b). Biotically dispersed acorns are usually transported far from adult oaks, and buried under shrubs or under other tree species (Gómez et al., 2003a; Gómez, 2003). Seedlings emerge during late spring and summer (Gómez, 2004). *Q. ilex* is a shade-tolerant species during early stages of its life-cycle (Espelta et al., 1995; Retana et al., 1999; Gómez-Aparicio et al., 2005b). However, shade tolerance estimated for *Q. ilex* is moderate (3.02 in a 0–5 scale according to Niinemets and Valladares, 2006), and it is a late successional tree in many Mediterranean conditions (Retana et al., 1999).

2.2. Data collection

Naturally emerged seedlings were marked during late spring and summer of 2001, 2002 and 2003. *Q. ilex* seedlings are easy to discover since they have big size and bright green colour. Thus, we searched for seedlings by running the entire 12-ha plot. After discovering a seedling it was permanently marked with a coloured flag. As our search was non-systematic, we marked seedlings per microhabitat haphazardly. This means that number of seedling marked per microhabitat and year was proportional to their abundance. Thus, the number of seedlings for this study was 67 seedlings in 2001, 78 seedlings in 2002 and 190 seedlings in 2003.

For each seedling we recorded irradiance from hemispherical photographs (Rich, 1990; Chen et al., 1991; Roxburgh and Kelly, 1995). Comparisons of methods revealed a good accuracy of hemispherical photography for the description of understory light availability, particularly in heterogeneous sites with a high number of gaps. In October 2003 photographs were taken above each seedling (whether alive or dead), at a height of

Table 1
Between-microhabitat differences in microclimatic and soil properties

Abiotic characterization	Oak woodland						Afforestation ^a
	Open	Subshrub	Broom	Tall Shrub	Oak	Pine	
Irradiance							
GSF ^b	0.58 ± 0.03	0.56 ± 0.04	0.45 ± 0.03	0.42 ± 0.02	0.44 ± 0.04	0.27 ± 0.01	0.17 ± 0.00
Radiation above (%) ^c	99.10 ± 0.64	57.10 ± 0.98					
Microclimate							
Temperature (°C) ^{c,d}	33.41 ± 0.53	29.51 ± 0.31		17.15 ± 0.37	18.72 ± 0.14	17.94 ± 0.21	17.94 ± 0.21
Temperature below (°C) ^c	32.40 ± 0.33	23.30 ± 0.21					
Relative humidity March (%) ^d	22.17 ± 1.77			24.52 ± 2.04	29.14 ± 1.58	24.06 ± 1.38	41.51 ± 2.11
Relative humidity July (%) ^d	1.84 ± 0.20			2.89 ± 0.24	4.38 ± 0.31	2.54 ± 0.25	4.70 ± 0.60
VWC below (%) ^c	8.73 ± 0.47	9.31 ± 0.40					
VPD (MPa) ^c	5.78 ± 0.14	2.94 ± 0.04					
Soil properties							
P (mg/kg) ^{c,f}	5.67 ± 0.54	8.07 ± 0.92	8.56 ± 0.53	10.58 ± 2.69	15.60 ± 3.31	5.10 ± 0.85	3.80 ± 0.29
N (%) ^{c,f}	0.35 ± 0.02	0.36 ± 0.02	0.33 ± 0.02	0.42 ± 0.03	0.80 ± 0.29	0.33 ± 0.04	0.14 ± 0.04
K (mg/kg) ^{c,e,f}	151.50 ± 9.46	215.50 ± 17.65	166.67 ± 9.65	196.75 ± 11.93	323.0 ± 35.5	137.0 ± 22.6	
Mg (cmol/kg) ^f	1.56 ± 0.10	2.44 ± 0.15		2.32 ± 0.33	4.25 ± 0.51	3.18 ± 0.21	
Ca (cmol/kg) ^{c,e,f}	14.65 ± 0.76	17.41 ± 0.85	13.88 ± 0.94	17.68 ± 1.21	27.39 ± 3.02	14.02 ± 1.51	
Na (cmol/kg) ^f	0.14 ± 0.08	0.05 ± 0.00		0.10 ± 0.03	0.08 ± 0.01	0.05 ± 0.00	
Organic carbon (%) ^d	5.27 ± 0.26			6.85 ± 0.97	17.36 ± 13.60	5.78 ± 0.48	2.38 ± 1.10
OOM (%) ^{c,e,f}	5.05 ± 0.40	5.65 ± 0.29	5.37 ± 0.40	6.51 ± 0.56	17.36 ± 4.30	5.78 ± 0.48	
CEC (cmol/kg) ^{c,e,f}	18.27 ± 1.16	9.56 ± 0.42	20.19 ± 1.27	12.18 ± 1.18	39.08 ± 4.90	19.03 ± 1.03	
Carbonates (%) ^f	3.42 ± 0.64	2.63 ± 0.35		2.54 ± 0.45	5.10 ± 1.00	2.73 ± 0.84	
AWC (%) ^{c,f}	17.34 ± 1.54	21.00 ± 0.60		22.43 ± 0.91	18.13 ± 0.91	16.86 ± 0.35	
pF 1/3 atm ^d	35.52 ± 0.62			35.41 ± 0.74	53.41 ± 18.02	32.48 ± 0.91	23.78 ± 0.84
pF 1/12 atm ^d	19.02 ± 0.84			19.55 ± 0.48	35.28 ± 5.55	15.62 ± 0.87	10.08 ± 0.49
pH ^{c,e,f}	7.43 ± 0.03	7.54 ± 0.06	7.13 ± 0.12	7.25 ± 0.07	7.35 ± 0.14	7.69 ± 0.03	
Clay (%) ^{c,e,f}	29.50 ± 0.85	29.80 ± 0.83	28.59 ± 1.06	27.86 ± 0.92	22.8 ± 1.4	22.6 ± 1.5	
Sand (%) ^{c,e,f}	23.66 ± 2.40	19.08 ± 0.85	24.74 ± 1.65	20.27 ± 2.01	17.4 ± 3.2	33.7 ± 1.9	
Soil compaction (MPa) ^e	4.84 ± 0.32	4.97 ± 0.24	5.36 ± 0.18	4.40 ± 0.28			

Note: Data show mean ± S.E. Blank cells mean no data available.

Abbreviations: GSF = Global Site Factor; VWC = Volumetric Water Capacity; VPD = Vapor Pressure Deficit; OOM = Oxidizable Organic Matter; CEC = Cation Exchange Capacity; AWC = Available Water Capacity.

^a The only microhabitat appearing in afforestation is pine (see Section 2).

^b This study.

^c Gómez-Aparicio et al. (2005a).

^d Gómez (2004).

^e Gómez-Aparicio et al. (2005b).

^f Puerta-Piñero et al. (2006).

0.25 m above the ground using a horizontally levelled digital camera (CoolPix 995 digital camera, Nikon, Tokyo, Japan) and aimed at the zenith, using a fish-eye lens of 180° field of view (FCE8, Nikon). All photographs were taken, either before dawn, after sunset, or at other times of the day when the sun was blocked by clouds, so an homogeneous illumination of the overstorey canopy and a correct contrast between the canopy and the sky was ensured. Photographs were analyzed using Hemiview canopy analysis software Version 2.1 (1999, Delta-T Devices Ltd., Cambridge, UK). This software is based on the program CANOPY (Rich, 1990). We chose the following irradiance variables: (1) direct (DSF); (2) indirect (ISF); (3) global (GSF) site factors. These factors are estimates of the fraction of direct, and diffuse or indirect radiation, respectively, expected to reach the spot where the photograph was taken (Anderson, 1964; Rich, 1990). The GSF combines direct radiation (DSF), by calculating the annual solar track, and diffuse radiation (ISF), based on a uniform overcast sky model (Clark et al., 2003) and represents the proportion of full sunlight

penetrating the forest canopy. These three variables are usually highly correlated, since they are related by the formula $GSF = 0.9(DSF) \pm 0.1(ISF)$. Thus, for subsequent analyses we chose GSF because it synthesizes more information.

At the time we found each seedling, the following co-variables, related to biotic seed dispersal, were also estimated for each seedling: (1) acorn presence, by digging the soil until we found the acorn or the remains of the cotyledon marks (if the acorn was removed); (2) acorn depth, the depth at which the acorn was found, in cm, from the insertion to the soil surface; (3) layer, as the type of layer in which the acorn was buried, whether litter or soil; (4) distance to oak, as the distance, in m, from the seedling to the nearest adult oak.

Finally, at the same time, we considered two performance traits: (1) seedling height, in cm, taken from the acorn insertion to the end of the seedling; (2) seedling survival. Seedling height was measured at the first time each seedling was found (field site was frequently and intensively explored for seedlings during late spring and summer). In this species most mortality

Table 2
Seedling performance in space and time

Effect	d.f.	Survival		Height		
		χ^2	<i>p</i>	SS	<i>F</i>	<i>p</i>
Landscape unit	2	0.032	0.9985	20.955	1.657	0.1754
Microhabitat [Landscape Unit]	11	21.436	0.0291	151.465	3.267	0.0002
Year (random)	2	15.516	0.0004	257.446	30.543	<0.0001
Likelihood χ^2	16	73.900	<0.0001	569.517	8.446	<0.0001
<i>R</i> ²		0.184		0.219		

Results of the multivariate model (log-linear model for survival and general linear model for height). Non-significant interaction terms were pooled with the degrees of freedom of the error term (Zar, 2006).

occurs after the first summer season (Rey Benayas, 1998; Gómez, 2004). Thus, we revisited each seedling after the first summer and registered the survival. Whenever possible, the cause of mortality was also recorded. Dead seedlings due to summer drought appeared visibly dried and brownish while ungulate damage was undoubtedly discernible by a clear cut on the shoot or by the complete absence of the seedling, with a remnant hole or tracers on the ground (Gómez et al., 2003a; Gómez, 2004; Gómez-Aparicio et al., 2004). Subsequently, for all the analyses we eliminated the seedlings dying from biotic causes (mainly from ungulates damage).

2.3. Data analysis

Spatio-temporal variability in seedling survival was analyzed by log-linear models, whereas seedling height was analyzed by general linear models. In these models landscape

unit, microhabitat nested within landscape unit and year (random) were considered as independent variables. The effects of each trait on seedling performance were tested by logistic (survival) or linear (height) multivariate regressions.

To determine the effect of each trait on survival and height while removing the confounding effects of the other traits, we used the partial regression leverage plots of each trait on residuals for seedling height and the proportion from the odd-ratios for seedling survival (Rawling et al., 1998). All data were analyzed using JMP 5.0 statistical package (SAS, 1997).

3. Results

There was a significant effect of spatial heterogeneity on seedling survival and height (Table 2). This effect was due to differences in microhabitat rather than landscape unit. Seedling survival was higher under oak, pine or tall shrub than under brooms or in open areas (Fig. 1, chart C). On the other hand, seedlings under tall shrubs, subshrubs or pines were taller than those growing under brooms, oaks or in open areas (Fig. 1, chart D). There were also significant differences in survival and height among years (Table 2). Seedling survival was higher in 2002 than in the other years (Fig. 1, chart A), while seedling height was significantly lower in 2003 than in the previous 2 years (Fig. 1, chart B).

Irradiance was on average ca. 0.30, that is, one third of that found in the open (see Table 1 for microhabitat-specific values). We found a significant negative effect of irradiance on seedling survival (Table 2; Fig. 2). In the multivariate model irradiance did not affect seedling height (Table 2). However, we found a significant quadratic simple relationship between seedling

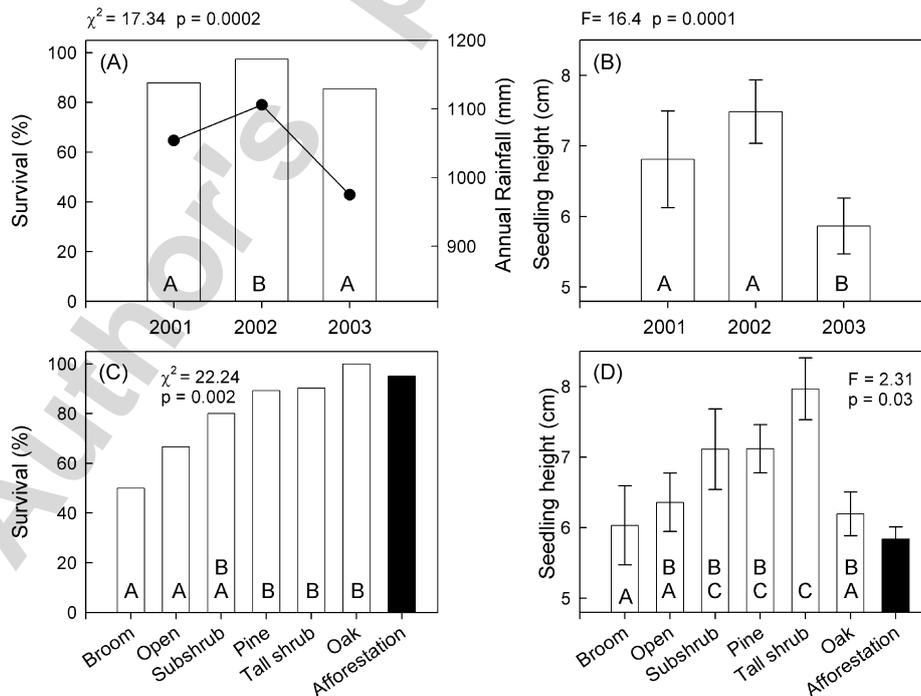


Fig. 1. Mean survival percentage for each microhabitat and years considered. Data show mean \pm S.E. of seedling height for each microhabitat year. White bars indicate different “oak-woodlands” microhabitats while black bar correspond to pine microhabitat under “afforestation”. Different letters designate significant differences in ANOVAs and χ^2 tests after the fixed Bonferroni correction. Black line shows mean annual rainfall in mm for each year. *N* = 335 seedlings.

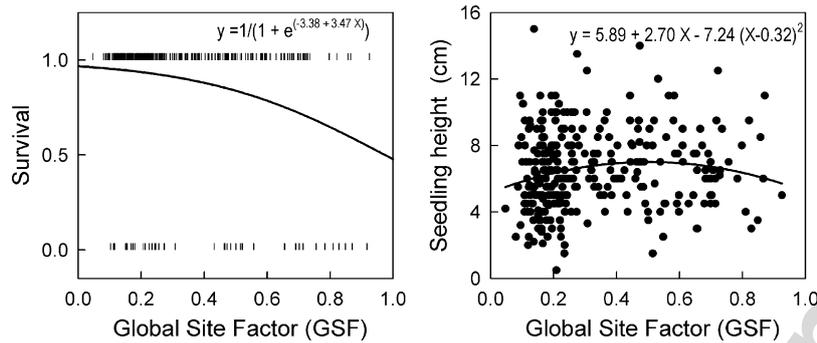


Fig. 2. Logistic regression between GSF vs. seedling survival on the left. Quadratic regression between GSF vs. seedling height on the right. $N = 335$ seedlings.

height and GSF ($F = 3.77$, $p = 0.02$, $R^2 = 0.02$, quadratic regression, Fig. 2). In both cases, maximum values of seedling height were obtained for GSF values near 0.5 (Fig. 2).

Seedling survival was also affected by acorn presence (Table 3), so seedlings with attached acorns survived significantly more than those without the remaining acorn. However, no significant relations were found between survival and acorn depth (Table 3), layer in which the acorns were sowed, or distance to oak (Table 3).

Seedling height was influenced by acorn presence (Table 3); seedlings with attached acorns grew more than those with no remaining acorn. In contrast to seedling survival, seedling height was also influenced by two other factors: layer in which the acorns were sowed (Table 3), hence acorns buried in soil were taller than acorns sowed in litter, and distance to nearest oak (Table 3), seedlings closer to the nearest adult growing more than further away.

4. Discussion

4.1. Seedling performance in space and time

Q. ilex seedling survival and growth varied spatially. Remarkably, spatial heterogeneity widely varied in our study site even within areas of a few square meters, since the most relevant spatial scale was the microhabitat. This heterogeneity has in the Mediterranean area in general, and in our study site in particular, a fine grain size (Gómez-Aparicio et al., 2005b). Consequently, plants face to a gradient of different quality sites for their subsequent fate. Considering the temporal responses of

this study, seedlings performed in the same way for survival and height. During years 2001 and 2002 seedling height was higher than in 2003; also, more seedlings were able to survive to summer drought (see Gómez-Aparicio et al., 2004 for similar temporal trends in the same area). These results, although not conclusive, were also related to inter-annual differences in mean precipitation between years (see Fig. 1, chart A), suggesting abiotic constraints in the temporal dimension. On the other hand, microhabitats seem to be the most important spatial explanatory factor. Furthermore, differences were significant both for seedling survival and growth. However, different microhabitats entail different signs in terms of survival or growth for the seedlings (see Maestre et al., 2001; Gómez-Aparicio et al., 2004, 2005b for similar results). For instance, in view of seedling survival, oak or pine microhabitats gained higher survival rates than brooms or open areas. At the same time, under oaks, brooms or in open areas seedling height was lower than under tall shrubs. Thus, some suitable microhabitats for survival (as oaks and pines) are, at the same time, inadequate for growth.

4.2. Effect of irradiance on seedling performance

Irradiance significantly influenced seedling survival and growth. Our results indicate that the less the irradiance the higher the seedling survival. At the same time, the better growth was found at intermediate irradiance exposures. In this system, influence of irradiance on survival exhibited a decisive pattern with survival decreasing for irradiances higher than 50%. While, in contrast, we found an optimum irradiance for growth

Table 3
Relative effects of irradiance on seedling performance

Effect	df	Seedling survival					Seedling height				
		$\beta \pm 1\text{S.E.}$	χ^2	p	R^2	%Var	$\beta \pm 1\text{S.E.}$	F	p	R^2	%Var
Acorn presence	1	0.361 \pm 0.171	4.464	0.035		0.183	0.286 \pm 0.133	4.607	0.033		0.229
Acorn depth	1	-0.038 \pm 0.180	0.046	0.831		0.065	0.052 \pm 0.134	0.151	0.698		0.000
Layer	1	0.171 \pm 0.191	0.807	0.369		0.063	0.443 \pm 0.139	10.111	0.002		0.371
Distance to oak	1	0.025 \pm 0.019	1.843	0.175		0.024	-0.035 \pm 0.012	9.180	0.003		0.357
GSF	1	-2.289 \pm 0.865	6.994	0.008		0.664	-1.018 \pm 0.749	1.846	0.175		0.043
Whole model	5		21.504	0.0007	0.080			7.031	<0.0001	0.085	

Summary of the multivariate regressions on seedling survival and height. R^2 's for seedling survival have been obtained from odd-ratios, whereas for seedling height R^2 's have been obtained from leverage plots. %Var refers to the proportion of the variance of the whole model R^2 explained by each independent variable.

ca. 50% of the irradiance gained in the open. These results support other studies in *Q. ilex* (Espelta et al., 1995; Broncano et al., 1998; Rey Benayas, 1998; Retana et al., 1999; Gómez-Aparicio et al., 2005b) with similar results for survival and growth being better at intermediate irradiance exposures than at higher levels. Among abiotic characteristics, reduction of irradiance has been emphasized as a main facilitation mechanism in Mediterranean-type ecosystems (Maestre et al., 2001; Gómez-Aparicio et al., 2005a). On the other hand, high irradiance levels have been proven to influence plant recruitment by altering photosynthesis efficiency, photoinhibition, biomass allocation, relative growth rate and survival (Faria et al., 1998; Retana et al., 1999; Valladares et al., 2000; Zavala et al., 2000; Oliveira and Peñuelas, 2002). Specifically in the case of *Q. ilex*, irradiance affect gas exchange (Gratani, 1997; Staudt and Bertin, 1998; Valladares et al., 2000; Gómez-Aparicio et al., 2005b), pigment composition (Valladares et al., 2000), survival, and relative growth rate (Rey Benayas, 1998; Gómez, 2004; Espelta et al., 1995; Gómez-Aparicio et al., 2005a,b). Thus, as either too shaded or very exposed sites are detrimental for seedling growth, moderate shade is crucial for seedling recruitment in this species. This implies that, in heterogeneous systems, seedlings deal with a gradient in irradiance that could translate into a mosaic of different quality sites. Consequently, natural regeneration in these types of heterogeneous systems (via survival or growth), appears to be superior compared to other homogeneous extreme systems (either with too high or too low irradiance levels).

The effect of irradiance on seedling performance could add an explanation to the spatial pattern observed in *Q. ilex* recruitment. However, summer drought and extreme temperatures have also been reported as important factors modelling Mediterranean plant recruitment (Blondel and Aronson, 1999). We argue that, as a rule, irradiance is highly correlated with temperature and water content (Clark et al., 2003), so our conclusions do not reject these other ideas. Different species can have different quality if they differentially modify key environmental variables influencing seedling establishment patterns (Tripathi and Khan, 1990; Gómez-Aparicio et al., 2004; Table 1, this study). Thus, different species-specific effects can alter microhabitats in terms of microclimate, soil properties or irradiance (Table 1) or even via different allelopathic relationships among plants (Puerta-Piñero et al., 2006). In this system different microhabitats differ in irradiance (Gómez et al., 2004; Gómez-Aparicio et al., 2005b; Table 1, this study). Thus, there are some microhabitats, such as brooms or open areas, where irradiance is too high and, consequently, harmful for the plants. So, these microhabitats, at the end, provide “bad-quality” sites for establishment. On the other hand, less irradiance appears under tall shrubs, pines or oaks where the conditions allow the seedlings to survive and thus, provide “good-quality” sites for establishment. Since intermediate irradiances are usually found under tall shrubs or subshrubs (Gómez et al., 2004), these types of microhabitats, in addition of being good for seedling survival, provide “good-quality” sites for seedling growth. In other words, these microhabitats can act as relevant

regeneration niches (*sensu* Grubb, 1977) for *Q. ilex* in the study site.

Our results can be extrapolated to the complete *Q. ilex* life cycle. Seedlings fate will depend on the exact place in which the seeds are hoarded. Other factors that had an effect on our model for seedlings survival and growth apart from irradiance (acorn presence, layer, depth at which acorns were buried and distance to the nearest adult oak) are also mainly due to biotic seed dispersal (Bosema, 1979; Sork, 1984; Gómez, 2003; Gómez et al., 2003b; Li and Zhang, 2003; Cheng et al., 2005; Den Ouden et al., 2005; author’s unpublished data). Of all these factors, acorn presence and distance to the nearest oak, according to the percent of variance explained, seem to be the most important ones. In the study area, seed deposition is mainly caused by jays and rodents (Gómez, 2003; Gómez et al., 2003b). Each species acts differently in terms of microhabitat of destiny, capacity of recovering the hoarded acorns and distance at which they cache them (Gómez, 2003; Gómez et al., 2003b; Den Ouden et al., 2005; authors’ unpublished data). This entails that the disperser identity can modulate the spatial pattern of *Q. ilex* populations in different ways. However, we also argue that, in heterogeneous systems, greater availability of “good-quality” sites may render other factors (i.e. acorn presence or distance to adults) to be of lesser importance than irradiance (Tripathi and Khan, 1990).

In conclusion, in heterogeneous landscapes, as in the Mediterranean region, irradiance can modify *Q. ilex* early recruitment by differences in the spatial dimension. These variations in seedling survival and performance are caused by a compendium of biotic and abiotic factors that generally interact with each other. Future studies should follow further stages on the *Q. ilex* ontogeny and should disentangle the role of each individual plant–plant and disperser–plant specific interaction on the dynamics of natural communities.

Acknowledgements

Daniel García kindly enhanced a preliminary version of this manuscript. Financial support was provided by the Spanish Ministry of Science and Education (fellowship FPU AP2003-3444 to C.P.P. and grants REN2003-07048 to J.M.G. and AGL2004-00536/FOR to F.V.). Red de Jardines Botánicos de Andalucía (Junta de Andalucía) and the headquarters of the Sierra Nevada National Park gave constant support and facilities for field work. The networks GLOBIMED (<http://www.globimed.net>) and REDBOME (<http://www.redbome.org>) facilitated the collaborative work.

References

- Anderson, M.C., 1964. Studies of the woodland light climate. The photographic computation of light conditions. *J. Ecol.* 52, 27–41.
- Beckage, B., Clark, J.S., 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84, 1849–1861.
- Blondel, J., Aronson, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, New York, USA.
- Bosema, I., 1979. Jays and oaks: eco-ethological study of a symbiosis. *Behaviour* 70, 1–117.

- Broncano, M.J., Riba, M., Retana, J., 1998. Seed germination and seedling performance of two Mediterranean tree species, Holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. *Plant Ecol.* 138, 17–26.
- Caldwell, M.M., Pearcy, R.W., 1994. Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above and Belowground. Academic Press, San Diego, CA, USA.
- Callaway, R.M., 1995. Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Chen, J.M., Black, T.A., Adams, R.S., 1991. Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. *Agr. For. Meteorol.* 56, 129–134.
- Cheng, J., Xiao, Z., Zhang, Z., 2005. Seed consumption and caching on seeds of three sympatric tree species by four sympatric rodent species in a subtropical forest, China. *For. Ecol. Manage.* 216, 331–341.
- Clark, J.M., Macklin, E., Wood, L., 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* 68, 213–235.
- Clark, J.S., Mohan, J., Dietze, M., Ibañez, I., 2003. Coexistence: how to identify trophic trade-offs. *Ecology* 84, 17–31.
- Den Ouden, J., Jansen, P.A., Smit, R., 2005. Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. In: Forget, P.-M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate*. CAB International, Oxfordshire, UK, pp. 223–239.
- Espelta, J.M., Riba, M., Retana, J., 1995. Patterns of seedling recruitment in west Mediterranean coppiced Holm-oak (*Quercus ilex* L.) forests as influenced by canopy development. *J. Veg. Sci.* 6, 465–472.
- Faria, T., Silvério, D., Breia, E., 1998. Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. *Physiol. Plant.* 102, 419–428.
- García, D., Obeso, J.R., Martínez, I., 2005. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *J. Ecol.* 93, 693–704.
- Gómez, J.M., 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* 26, 573–584.
- Gómez, J.M., 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. *Plant Ecol.* 192, 287–297.
- Gómez, J.M., García, D., Zamora, R., 2003a. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For. Ecol. Manage.* 180, 125–134.
- Gómez, J.M., Márquez, R., Puerta Piñero, C., 2003b. Interacciones entre la encina *Quercus ilex* y el ratón de campo *Apodemus sylvaticus*: mutualismo o antagonismo? In: *Proceedings of VII AEET Conference* (Ed AEET), Barcelona, Spain, pp. 14–24.
- Gómez, J.M., Valladares, F., Puerta-Piñero, C., 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. *Funct. Ecol.* 18, 787–792.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., 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.
- Gómez-Aparicio, L., Gómez, J.M., Zamora, R., Boettinger, J.L., 2005a. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *J. Veg. Sci.* 16, 191–198.
- Gómez-Aparicio, L., Valladares, F., Zamora, R., Quero, J.L., 2005b. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. *Ecography* 28, 757–768.
- Gratani, L., 1997. Canopy structure, vertical radiation profile and photosynthetic function in a *Quercus ilex* evergreen forest. *Photosynthetica* 33, 139–149.
- Grubb, P.J., 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145.
- Hutchings, M.J., John, E.A., Stewart, A.J.A., 2000. *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Sciences, Oxford, UK.
- Hutchings, M.J., John, E.A., Wijesinghe, D.K., 2003. Toward understanding the consequences of soil heterogeneity for plant populations and community. *Ecology* 84, 2322–2334.
- Kitajima, K., Fenner, M., 2000. Ecology of seedling regeneration. In: Fenner, M. (Ed.), *Seed: The Ecology of Regeneration in Plant Communities*. 2nd ed. CAB International, Oxfordshire, UK, pp. 331–359.
- Li, H.J., Zhang, Z.B., 2003. Effect of rodents on acorn dispersal and survival of Liaodong oak (*Quercus liaotungensis* Koidz). *For. Ecol. Manage.* 176, 387–396.
- Maestre, F.T., 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.
- Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought and water-logging of temperate, Northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Oliveira, G., Peñuelas, J., 2002. Comparative protective strategies of *Cistus albidus* and *Quercus ilex* facing photoinhibitory winter conditions. *Environ. Exp. Bot.* 47, 281–289.
- Pearcy, R.W., 1999. Responses of plants to heterogeneous light environments. In: Pugnnaire, F.I., Valladares, F. (Eds.), *Handbook of Functional Plant Ecology*. Marcel-Dekker Inc., New York, USA, pp. 269–314.
- Puerta-Piñero, C., Gómez, J.M., Zamora, R., 2006. Species-specific effects on topsoil development affect *Quercus ilex* seedling performance. *Acta Oecol.* 29, 65–71.
- Pugnnaire, F.I., Valladares, F., 1999. *Handbook of Functional Plant Ecology*. Marcel-Dekker Inc., New York, USA.
- Pulido, F., Díaz, M., 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. *Écoscience* 12, 92–102.
- Rawling, J.O., Pantula, S.G., Dickey, D.A., 1998. *Applied Regression Analysis, A Research Tool*. Springer, New York, USA.
- Retana, J., Espelta, J.M., Gracia, M., Riba, M., 1999. Seedling recruitment. In: Rodá, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), *Ecology of Mediterranean Evergreen Oak Forests*. Springer-Verlag, Berlin, pp. 89–103.
- Rey Benayas, J.M., 1998. Growth and survival in *Quercus ilex* L. Seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural land. *Ann. Sci. For.* 55, 801–807.
- Rich, P.M., 1990. Characterizing plant canopies with hemispherical photographs. *Remote Sens. Rev.* 5, 13–29.
- Roxburgh, J.R., Kelly, D., 1995. Uses and limitations of hemispherical photography for estimating forest light environments. *NZ J. Ecol.* 19, 213–217.
- SAS Institute Inc., 1997. *SAS/STAT Software: Changes and Enhancements Through Release 6.12*. SAS Institute Inc., Cary, NC.
- Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Écoscience* 2, 267–275.
- Silvertown, J.W., Charlesworth, D., 2001. *Introduction to Plant Population Biology*. Blackwell Science, New York.
- Sork, V.L., 1984. Examination of seed dispersal and survival on red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. *Ecology* 65, 1020–1022.
- Staudt, M., Bertin, N., 1998. Light and temperature dependence of the emission of cyclic and acyclic monoterpenes from Holm oak (*Quercus ilex* L.) leaves. *Plant Cell Environ.* 21, 385–395.
- Tripathi, R.S., Khan, M.L., 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* 57, 289–296.
- Turton, S.M., Duff, G.A., 1992. Light environments and floristic composition across an open forest-rainforest boundary in northeastern Queensland. *Aust. J. Ecol.* 17, 415–423.
- Valladares, F., 2003. Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. In: Esser, K., Lüttge, U., Beyschlag, W., Hellwig, F. (Eds.), *Progress in Botany*. Springer-Verlag, Heidelberg, pp. 439–471.
- Valladares, F., 2004. *Ecología del bosque mediterráneo en un mundo cambiante. Naturaleza y Parques Nacionales. Serie Técnica*. Ministerio de Medio ambiente, Organismo Autónomo Parques Nacionales, Madrid, Spain.
- Valladares, F., Guzmán, B., 2006. Canopy structure and spatial heterogeneity of understory light in abandoned Holm oak woodlands. *Ann. For. Sci.* 63, 749–761.
- Valladares, F., Martínez-Ferri, E., Balaguer, L., Pérez-Corona, E., Manrique, E., 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? *New Phytol.* 148, 79–91.

- Watling, J.R., Press, M.C., 2000. Light heterogeneity in tropical rain forests: photosynthetic responses and their ecological consequences. In: Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science, Oxford, pp. 131–154.
- Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science, Oxford, pp. 9–31.
- Zar, J.H., 2006. *Biostatistical Analysis*. Prentice-Hall, New Jersey, USA.
- Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean plant communities. The case of Holm oak–Aleppo Pine forests. *Bot. Rev.* 66, 119–149.

Author's personal copy