Original article

Seedling survival responses to irradiance are differentially influenced by low-water availability in four tree species of the Iberian cool temperate–Mediterranean ecotone

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ARTICLE INFO

ABSTRACT

Inter-specific differences in seedling survival responses along a sun-shade gradient and the influence of low-water availability were examined for four Iberian tree species (*Quercus robur* L., *Quercus pyrenaica* Willd., *Pinus sylvestris* L. and *Pinus pinaster* Ait.) typical of the cool temperate–Mediterranean transition zone. Seedlings were grown under controlled conditions in a factorial experiment with four levels of irradiance (1%, 6%, 20% and 100% of full sunlight) and two levels of water availability. Five censuses (from late spring to autumn) leading to four regular intervals ($T_0 \rightarrow T_I$; $T_I \rightarrow T_{II}$; $T_{II} \rightarrow T_{III}$; $T_{III} \rightarrow T_{IV}$) were established. Statistical models of seedling survival as a function of irradiance were calibrated throughout the whole experiment ($T_0 \rightarrow T_{IV}$) and also for each time interval and water availability level. Seedling survival responses among different species diverged both in the type of functional response to irradiance and in their response to water stress. Ranking of species according to shade tolerance (*Q. pyrenaica* > *Q. robur* > *P. sylvestris* > *P. pinaster*) contrasted with tolerance of high irradiance and conformed to a hypothetical sun-shade trade-off for survival (i.e. species having higher survival in low irradiance—oaks—had poorer survival at high irradiance and vice-versa). Low-water availability also differentially affected each species, with pines being more drought tolerant than oaks. At an intra-specific level, low-water availability decreased survival of *Q. pyrenaica* under both high and low irradiance. For *Q. robur*, however, low-water availability exerted a relatively stronger effect under low irradiance. Consequences of the interplay between irradiance and water availability for explaining segregation and coexistence of forest tree species at the ecotone between cool temperate and Mediterranean forests are discussed.

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1. Introduction

Understanding how species respond to resource availability is central for the development of an explanatory and predictive plant ecology (Mooney, 1972; Bazzaz, 1979; Tilman, 1988).

Along a productivity gradient, forest composition is largely governed by tolerance to the most limiting resource in a given part of the gradient (Denslow, 1987; Chazdon, 1988; Valladares, 2003). At the upper end of this gradient, light becomes the most important limiting resource for establishment, growth and survival of juvenile individuals and inter-specific differences in juvenile responses to light largely explain niche differentiation along a succesional axis (Horn, 1971; Bormann and Likens, 1979; Shugart, 1984; Glizenstein et al., 1986; Pacala et al., 1996). At the lower end of the pro-

ductivity gradient (e.g. water limited plant communities) theoretical studies suggest that community composition is expected to be controlled by inter-specific differences in drought tolerance (Tilman, 1988; Smith and Huston, 1989). In particular, inter-specific differences in seedling tolerance of water stress are considered to be of paramount importance for explaining species distribution limits at the boundary of mesic and xeric plant communities (Keeley, 1992; Barton, 1993; Pigott and Pigott, 1993). However, the notion that only one resource is limiting at a time is presumably too simplistic given the increasing evidence that multiple limiting factors can co-occur in forest systems (Valladares and Pearcy, 1997; Valladares and Pearcy, 2002; Valladares et al., 2004; Engelbrecht et al., 2006). Thus, the interest of many ecologists is to understand how multiple factors interact and influence the performance of forest species. In particular, the study of interactive effects between light and water availability have been a central topic of a number of recent experimental studies (Sack and Grubb, 2002; Sack et al., 2003; Niinemets and Valladares, 2004; Sack, 2004; Aranda et al., 2005; Castro-Diez et al., 2006).

In the Iberian Peninsula a sharp climatic boundary in the North defines a transition between cool temperate and Mediterranean forests (see Gavilán and Fernández-Gonzalez, 1997). Because of topographic (e.g. altitudinal and slope aspect) gradients and microclimatic variation, species of both climatic types can coexist within relatively local scales in Southern localities (Costa et al., 1998). In these ecotone forests, both light and water limitations interact to control patterns of seedling establishment and subsequent stand dynamics (Holmgren, 2000; Zavala et al., 2000; Gómez-Aparicio et al., 2004). Thus, understanding survival responses to gradients of irradiance and water availability is critical for explaining shifts in species distributions along disturbance and environmental gradients (Pigott and Pigott, 1993).

Although the interplay between radiation and soil moisture has long been recognized as a critical process governing stand dynamics in the Mediterranean region (Olazábal, 1916), our knowledge of species responses to light and soil moisture is fragmentary and existing information is based on qualitative observations (Barnes et al., 1998) and a combination of different types of ecophysiological studies. Some of these latter studies have focused on plant water relations (e.g. Cochard, 1992; Aranda et al., 2001; Corcuera et al., 2002), leaf-level physiology (e.g. Gross et al., 1996; Hansen et al., 2002; Awada et al., 2003) and on general ecophysiology and whole plant allometry (e.g. Valladares et al., 2002; Sack, 2004; Valladares et al., 2005).

Only recently have quantitative computational or analytical methods been developed that allow us to establish effective comparisons of whole plant responses across species and sites (e.g. Pacala et al., 1994; Kobe et al., 1995; Hilborn and Mangel, 1997; Kobe, 1999; Beckage and Clark, 2003).

The main objectives of this study were: i) to test for species-specific responses in seedling survival along an irradiance gradient and to describe the functional responses observed, ii) to examine how low-water availability influences seedling survival responses to irradiance (i.e. shade tolerance and survival at high irradiance) both at the intra- and inter-specific level and, finally iii) to discuss the signifi-

cance of these responses for explaining patterns of tree segregation and coexistence in Iberian cool temperate–Mediterranean transition zone.

Seedling survival models can be calibrated with maximum likelihood techniques for a given species, water treatment and temporal interval to describe performance of an "average" seedling in a given microenvironment (Kobe, 1999). Such approximation avoids the need for data transformation which can obscure patterns that are amenable to biological interpretation (Hilborn and Mangel, 1997; Kobe, 1999). Standard survival analyses, logit analyses or hypotheses testing through general linear models require data to be transformed in some way. In addition, model flexibility is required to include explicitly irradiance as an independent variable in the mortality analyses and identify strategic axes along which species differentiate (see Pacala et al., 1996; Kobe, 1999). Emphasis on the study of seedlings is justified since seedling stage is considered as the life-history stage in which selective pressures are highest (Reich et al., 2003).

2. Materials and methods

2.1. Experimental design and study site

The experimental setting was based on a factorial design with three factors: irradiance, water availability and species. The four species are typical of the cool temperate–Mediterranean Iberian transition forests (*Quercus robur* L., *Quercus pyrenaica* Willd., *Pinus sylvestris* L. and *Pinus pinaster* Ait.) and dominate the forest overstory in this region along a geographic and environmental (productivity) gradient associated with the availability of water (Costa et al., 1998): from cool temperate (*Q. robur*) to mesic or montane (*Q. pyrenaica* and *P. sylvestris*) to Mediterranean (*P. pinaster*) forests. Species nomenclature followed (Tutin et al., 2001). The experiment was conducted from February till November 2001. Seeds and acorns were collected from different Spanish localities in 1999: *Q. robur* from Galicia, *Q. pyrenaica* from Sierra de Guadarrama, Madrid, *P. sylvestris* and *P. pinaster* from Sierra de Gredos, Ávila. Seedlings were grown at a commercial nursery (Viveros Barbol, Torremocha del Jarama, Madrid, Spain). The area was located at 40°50′N, 3°29′W and at 710 m a.s.l. Climate was continental Mediterranean with hot and dry summers and cold winters. Mean maximum and minimum temperature were 19 and 9.5 °C, respectively. Most annual rainfall (350–500 mm) is received during spring and fall (250–350 mm) (Instituto-Nacional-de-Meteorología, 2001). Soil substrate (pH 6.5) was a standard mixture used in native plant nurseries for seedlings production. This substrate consisted of 3:1 volume mixture of peat Vriezenveen PP1 (Potgrond Vriezenveen B.V., Westerhaar, the Netherlands) and washed river sand. We also added 3 kg m^{-3} of Guanumus Angibaud fertilizer (3-35-2 NPK, Angiplant, La Rochelle Cedex, France) and 2 kg m^{-3} of Plantacote mix 4 M fertilizer (15-10-15 NPK, Aglukon Spezialdünger GMBH & Co. KG, Dusseldorf, Germany).

Seedlings were germinated in February and March 2001 and were transplanted to forest multi-pot (330 cm³ each pot) containers in early spring. Local air temperature and available photosynthetic photon flux density (PPFD) were registered every 5 min during the whole growing season with a data logger (HOBO model H08-006-04, Onset, Pocasset, MA, USA) and external sensors cross-calibrated with a Li-Cor 190SA sensor (Li-Cor, Nebraska, USA). Mean daily PPFD over the summer was 42 mols m² day⁻¹. Four irradiance levels (1%, 6%, 20% and 100% of full sunlight) were established by using layers of neutral shade cloth supported by metal frames (one shade frame for each light level). This gradient spans over the natural range of light availability found in Iberian forest understories, 20% being the most common shade under Mediterranean forest canopies and 6% of full sunlight being relatively frequent in humid and sub-humid temperate forests (Gómez et al., 2004; Valladares, 2004). Light availability equivalent to 1% of full sunlight is typically found in other habitats like tropical and temperate forests (Canham et al., 1990) and also in sub-Mediterranean forests that experience moderate drought (Gratani, 1997). Thus, 1% of full sunlight was included to determine seedling response to light across the full irradiance availability gradient that can be encountered in the field. Air mean temperature during the experiment was similar (± 1 °C) across different irradiance environments. For example, in the hottest month of the year (i.e. July) mean temperature varied from (25.66 ± 0.17 °C) in 100% irradiance treatment to (24.43 ± 0.14 °C) in 6% irradiance treatment (mean temperature and standard error, respectively, are indicated). Two categorical watering levels were established by means of differences in irrigation intensity. We compensated for increasing evapotranspiration under increasing irradiance levels by adjusting irrigation intensity for each irradiance level to reduce uncontrolled interactions among irradiance and water availability (e.g. lower water availability under high irradiance). Seedlings were watered every second day with different irrigation intensity for each treatment (Table 1). Differences in water availability across irradiance levels were monitored by estimation of soil volumetric water content (Table 1) with an Aquaterr Moisture meter (model EC-200,

Aquaterr Instruments, Fremont, CA). This is a capacitance probe which measures the dielectric constant of the soil–air–water combination. A lower frequency in the irrigation regime (henceforth "low-watered" treatment) resulted in soil moisture values 14% lower than those reached under well-watered conditions. Within each combination of irradiance level and species (88 seedlings), each half (i.e. 44 seedlings) was allocated to a different irrigation regime (well-watered and low-watered treatment). Seedlings were arranged in six blocks randomly distributed within each irradiance level. Blocks were randomly rearranged within their corresponding treatments every week.

We carried out a total of five mortality censuses leading to four regularly spaced time intervals from June 14 to October first (2001) at 3.5–4 weeks each. Intervals are referred thereafter as: ($T_0 \rightarrow T_I$) spring–summer (14 June–10 July), ($T_I \rightarrow T_{II}$) summer (11 July–9 August), ($T_{II} \rightarrow T_{III}$) late summer (10 August–3 September) and ($T_{III} \rightarrow T_{IV}$) autumn (4 September–1 October). Individual performance of each seedling was evaluated at the end of each of these four intervals. Individuals that had lost all their aerial structure, did not have any photosynthetically active leaf (i.e. green leaves that were still-hydrated and pliable), or exhibited brittle stem (easily broken by finger pressure) at the upper third, were recorded as dead.

Seedlings were sprayed with a fungicide solution (50% Carbendazyme, Fungicida Polivalente, COMPO Agricultura SL, Barcelona) twice during the experiment in order to control fungal infections. None of the mortality events showed signs of fungal infection-mediated death.

2.2. Model calibration and statistical analysis

We formulated data-specific statistical models of seedling survival as a function of irradiance for each of the two watering levels. First, we examined survival at the end of the experiment (i.e. number of dead seedlings at the end of the experiment related to the number of seedlings that started the experiment). Also we formulated specific models for each of the four intervals considered to account for non-constant mortality rates due for example to ontogenetic changes that can be critical during the first year (e.g. based on seed size differences), cumulative water stress effects or other effects. Models were designed to account for patterns observed in our data set and to reflect alternative hypotheses regarding survival responses to irradiance. Models were calibrated and compared based on maximum likelihood estimation (Edwards, 1992). Survival at a given time interval is described as a binomial random variable. For n independent trials the likelihood function has the following general expression:

$$L = \prod_{i=1}^{n} p_i^{y_i} (1 - p_i)^{1-y_i} \tag{1}$$

where n is the total number of seedlings growing at the beginning of the interval, y_i is the value of the binomial variable for seedling i (one if the seedling i has survived at the end of a given interval and zero if the seedling has died). Assumptions of independency among observations are based on experimental design which includes seedling indi-

Table 1 – Percentage of gravimetric water content measured with a capacitance probe from June to September (four times evenly distributed within this time period) and irrigation intensity. A total of 15–20 pots per treatment (water × irradiance combination) were measured. Mean and standard error for maximum soil water content and difference between water treatments for each water × irradiance level combination are shown. Irrigation intensity (time in minutes) for each water × irradiance level combination is showed in brackets

Water treatments	Well-watered	Low-watered	Difference between water treatments
Irradiance			
100%	69.5 ± 1.7 (60)	56.5 ± 5.2 (30)	13.0 ± 3.5
20%	73.0 ± 2.9 (40)	58.8 ± 3.2 (10)	14.3 ± 2.5
6%	71.3 ± 5.6 (20)	60.3 ± 2.4 (5)	11.0 ± 4.1
1%	80.0 ± 2.1 (20)	63.0 ± 6.8 (5)	17.0 ± 5.0

vidual containers and spatial and temporal rearrangement of seedling containers. Survival probability within one interval is given by p_i. We explored a number of functional responses as suggested from our data and previous knowledge of whole plant responses to light. For our data set, the Michaelis–Menten (MM) function resulted in the best fit and was easier to interpret biologically relative to other functions explored (e.g. logistic curve). Thus seedling probability of mortality was described as:

$$p_i(La) = \frac{\alpha_0 La}{\frac{\alpha_0}{\alpha_1} + La} \qquad (2)$$

where p_i describes survival probability of seedling i, α_0 and α_1 are model parameters and La is irradiance. The parameter α_0 (asymptote) is delimited between 0 and 1 and describes maximum survival probability. Thus, species success at increasing irradiance levels is described by higher α_0 values. The parameter α_1 (always positive) is the slope of the survival curve at low irradiance. Large α_1 values reflect high tolerance of shade. Consequently, the model reduces to parameters α_0 and α_1 which describe two independent functional responses in seedling survival at high and low irradiance, respectively. We also tested for a non-zero (NZ) irradiance intercept. This is a shade tolerance strategy associated with low irradiance compensation rates by incorporating another parameter (β). A significant value for β (irradiance compensation point) implies a decrease in shade tolerance in relation to the basic MM function since it pushes the MM function towards the right end of the irradiance gradient. The modified MM function was:

$$\begin{cases} p_i(La) = \dfrac{\alpha_0(La - \beta)}{\dfrac{\alpha_0}{\alpha_1} + (La - \beta)} & x \geq \beta \\ p_i(La) = 0 & x < \beta \end{cases} \qquad (3)$$

This function derived from the MM function is called hereafter as NZ compensation point function. We evaluated the statistical effects of irradiance on seedling survival for each species by comparing models with irradiance dependency against a null model (NM, non-irradiance dependence, $p_i = \theta$) that implied constant probability of survival throughout the gradient. All models describing functional responses to irradiance were repeated for the two watering levels considered (well-watered and low-water conditions). The effect of low-water availability on seedling performance can be assessed by changes in the functional responses of seedling survival along the irradiance gradient: from a flat response (NM model) to a non-linear increase, or as changes in model parameters under both well-watered and low-water conditions. For example, changes in α_0 if the species follows the MM or the NZ model, or changes in α_1 or β if the species follows the MM or the NZ model. The resulting non-linear likelihood functions do not have obvious analytical solutions therefore we implemented a Markov Chain Monte Carlo numerical algorithm (e.g. Chib and Greenberg, 1995) to estimate parameters for each species, treatment and time interval (implemented in C++, Borland International Inc., 1996, v. 5.01). Nested models were compared with a likelihood ratio test (0.05 level), in which the degrees of freedom were

equal to the difference in the number of parameters between models (Edwards, 1992) and non-nested models were compared through Akaike Information Criterion (Hilborn and Mangel, 1997). When appropriate convergence methods and model parameters were normalized to prevent seedling survival function reaching values beyond the allowed domains (e.g. probability greater than 1). Confidence intervals were estimated by conducting a likelihood profile (Hilborn and Mangel, 1997), computing the differences in log-likelihood between 65,000 random parameter combinations and the highest likelihood estimate. The authors will provide further details including C++ coding upon request.

3. Results

3.1. Inter-specific differences in survival response to irradiance under well-watered conditions

Seedling survival differed across species, and depended on irradiance, water supply and time interval. Under well-watered conditions irradiance did not have a statistically significant effect on survival for either of the two oaks throughout the whole experiment ($T_0 \rightarrow T_{IV}$) (Fig. 1) and survival for these two species was best described by the NM (non-irradiance dependence, $p_i = \theta$) (Table 2). In contrast, irradiance had a statistically significant effect on both pines which fitted the NZ model (Table 2, $P < 0.05$, likelihood ratio test).

The impact of irradiance and species on survival was variable through time (Table 3 and Fig. 2). During the first interval ($T_0 \rightarrow T_I$) irradiance did not have a significant effect on any species (NM, non-irradiance dependence model for all species, $p_i = \theta$). Values of θ, however, differed significantly across species (see Table 3, non-overlapping confidence intervals for Q. robur and P. pinaster). During the summer interval ($T_I \rightarrow T_{II}$), survival of P. pinaster seedlings increased with irradiance ($P < 0,05$, likelihood ratio) according to the NZ model (Fig. 2 and Table 3). The effect of irradiance on the rest of species was negligible. In the late summer interval ($T_{II} \rightarrow T_{III}$), irradiance had a statistically significant effect on all species except Q. pyrenaica. During this period Q. robur and P. sylvestris followed the MM model and P. pinaster fitted the NZ model (Table 3). Finally, during the autumn interval ($T_{III} \rightarrow T_{IV}$), both pine species followed the irradiance-dependent MM model while the two oak species fitted the NM. Survival at high irradiance (α_0, MM and NZ models and θ for the NM) evaluated throughout the experiment ($T_0 \rightarrow T_{IV}$) unchanged in pines while it decreased significantly over time for oaks (e.g. θ at first and last interval for Q. pyrenaica and Q. robur ranged between 0.99–0.93 and 1.00–0.96, respectively, see Table 3).

3.2. Impact of low-water conditions on survival response to irradiance

Low-water availability modified species responses to irradiance for the different time intervals considered, but only
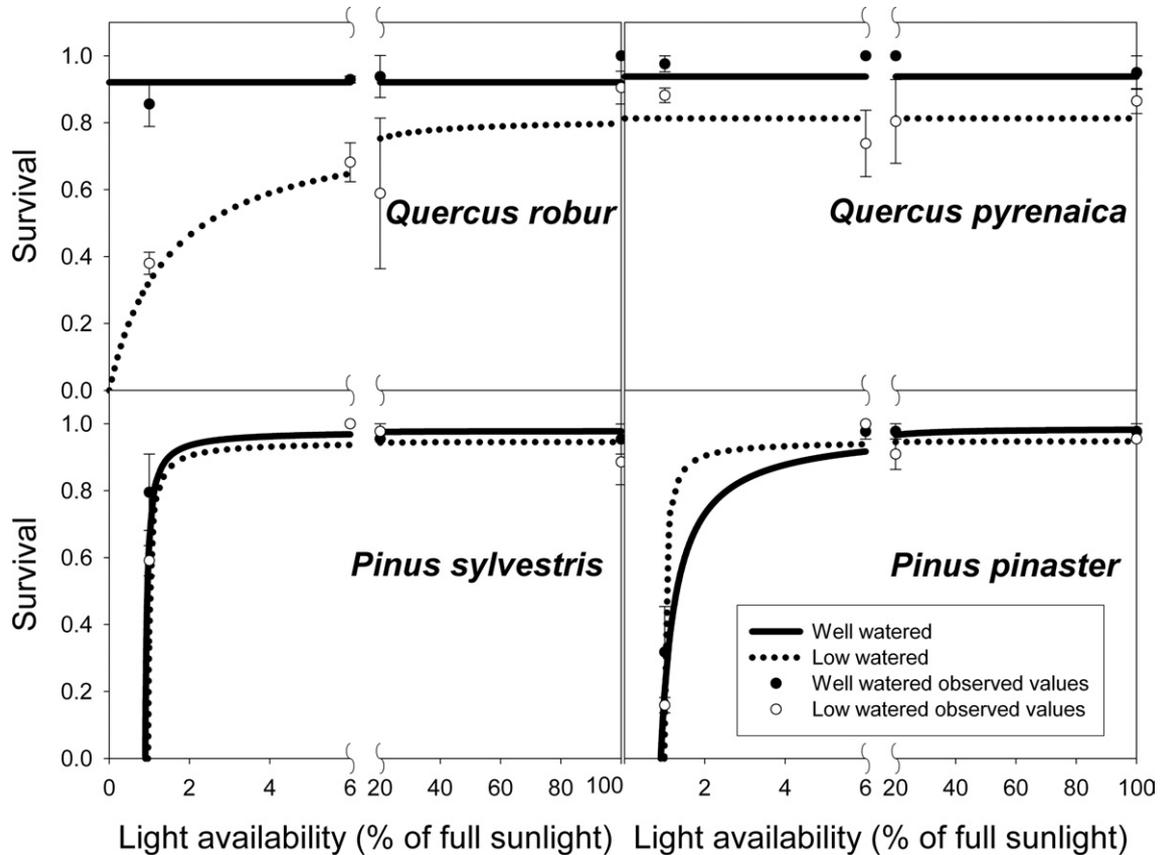
Fig. 1 – Models resulting in the best fit for seedling survival along the irradiance gradient and two levels of water availability. Survival was evaluated at the end of the experiment ($T_0 \to T_{IV}$). Mean and standard error for observed values are also shown. Length of the considered interval = 109 days, N = 44.

Table 2 – Maximum likelihood parameter estimates and 95% CI for survival model ($T_0 \to T_{IV}$) that resulted in the best fit to the data. Models were parameterized for each species and water availability level. Parameter addition in nested models resulted in a statistically significant better fit with respect to the NM ($P \leq 0.05$; likelihood ratio test). Models are coded as: NM, NZ intercept and MM. The third column shows values of θ for the NM or α_0 for other models. Values in bold indicate statistically significant differences in parameter values between water treatments (likelihood profile, $P < 0.05$)

Species	Best model	α_0; θ (95% CI)	α_1 (95% CI)	β (95% CI)
Well-watered				
Q. robur	NM	0.921 (0.912–0.929)		
Q. pyrenaica	NM	0.938 (0.934–0.938)		
P. sylvestris	NZ	0.978 (0.945–0.995)	19.397 (3.189–19.994)	0.900 (0.268–0.940)
P. pinaster	NZ	0.986 (0.933–1.000)	2.576 (0.896–19.912)	0.903 (0.626–0.991)
Water-stressed				
Q. robur	MM	0.809 (0.776–0.875)	0.543 (0.286–1.147)	
Q. pyrenaica	NM	0.813 (0.807–0.859)		
P. sylvestris	NZ	0.946 (0.901–0.977)	19.803 (3.363–19.992)	0.967 (0.784–0.982)
P. pinaster	NZ	0.948 (0.902–0.978)	19.405 (2.944–19.975)	0.996 (0.966–0.999)

had a significant impact on shade tolerance for one of the four species. Under well-watered conditions, irradiance had a statistically significant effect on survival of Q. robur seedlings across the whole observation period ($T_0 \to T_{IV}$) which increased non-linearly with irradiance (MM model). The resulting model implied a lower tolerance of shade but also a poorer performance under high irradiance (lower α_0 with respect to θ in the NM for well-watered conditions, Table 2). In contrast, under well-watered conditions, there was no sig-

nificant effect of irradiance on survival of Q. pyrenaica seedlings (Table 2). Low-water availability significantly impacted on the shade tolerance of Q. robur (shift from NM to MM function under water-stressed conditions; likelihood ratio test; $P < 0.05$, Table 2) whilst the effect of low-water availability on Q. pyrenaica was on overall survival. In the latter case the type of function did not change under water-stressed conditions but did change the parameter values (see Table 2 and Fig. 1). In contrast, seedlings of P. sylvestris and P. pinaster

Table 3 – Maximum likelihood parameter estimates and 95% CI for survival models that best fitted the data for the three last intervals. Models were parameterized for each species and water availability level. Parameter addition in nested models resulted in a statistically significant better fit with respect to the NM ($P \leq 0.05$; likelihood ratio test). Models are coded as: NM, NZ intercept and MM. The third column shows either θ values (NM) or α_0 (NZ or MM models). Values typed in bold indicate statistically significant differences in parameter values between water treatments (likelihood profile, $P \leq 0.05$)

Species	Best model	Well-watered conditions			Best model	Low-watered conditions		
		α_0; θ (95% CI)	α_1 (95% CI)	β (95% CI)		α_0; θ (95% CI)	α_1 (95% CI)	β (95% CI)
Interval I								
Q. robur	NM	1.000 (0.992–1.000)			NM	0.972 (0.965–0.973)		
Q. pyrenaica	NM	0.994 (0.983–0.998)			NM	0.977 (0.960–0.982)		
P. sylvestris	NM	0.989 (0.974–0.993)			NM	0.983 (0.977–0.983)		
P. pinaster	NM	0.983 (0.961–0.988)			NM	0.983 (0.980–0.987)		
Interval II								
Q. robur	NM	0.994 (0.994–0.999)			MM	0.901 (0.883–0.918)	1.834 (0.920–4.624)	
Q. pyrenaica	NM	1.000 (0.999–1.000)			NM	0.924 (0.900–0.925)		
P. sylvestris	NM	0.994 (0.987–0.994)			NZ	0.984 (0.955-0.998)	19.984 (3.777–19.991)	0.856 (0.125–0.924)
P. pinaster	NZ	0.999 (0.985–1.000)	19.582 (4.328–19.993)	0.946 (0.718–0.964)	NZ	0.971 (0.934–0.993)	18.247 (2.311–19.983)	0.911 (0.222–0.955)
Interval III								
Q. robur	MM	0.996 (0.992–0.996)	7.714 (3.448–19.992)		MM	0.946 (0.945–0.950)	2.828 (1.217–13.044)	
Q. pyrenaica	NM	1.000 (0.992–1.000)			NM	0.956 (0.954–0.962)		
P. sylvestris	MM	1.000 (0.992–1.000)	5.162 (2.710–11.068)		MM	1.000 (0.975–1.000)	5.222 (2.552–14.790)	
P. pinaster	NZ	0.999 (0.985–1.000)	19.818 (4.432–19.994)	0.928 (0.538–0.964)	NZ	0.999 (0.985–1.000)	19.750 (4.419–19.995)	0.982 (0.882–0.992)
Interval IV								
Q. robur	NM	0.965 (0.960–0.976)			MM	0.980 (0.970–0.997)	3.162 (1.329–12.603)	
Q. pyrenaica	NM	0.938 (0.901–0.939)			NM	0.875 (0.873–0.876)		
P. sylvestris	MM	1.000 (0.992–1.000)	6.745 (3.14–17.290)		MM	1.000 (0.991–1.000)	2.866 (1.517–6.102)	
P. pinaster	MM	1.000 (0.993–1.000)	2.435 (1.187–5.508)		NZ	0.992 (0.970–1.000)	18.859 (3.929–19.941)	0.962 (0.664–0.987)

did not experienced significant changes in their responses to irradiance with respect to well-watered conditions.

Across the four time intervals low-water availability resulted in both qualitative (i.e. different model) and quantitative (i.e. significant differences for the parameter values) changes in survival responses (see details in Table 3). For example, qualitative changes during the second interval ($T_I \rightarrow T_{II}$) resulted in both Q. robur and P. sylvestris shifting from the NM to the irradiance dependence model (MM and NZ, respectively) while in the fourth interval ($T_{III} \rightarrow T_{IV}$), Q. robur changed from the non-dependence model (NM) towards a dependence MM model and P. pinaster from MM to a NZ dependency model. Even when the species followed the same model both under well-watered and low-water conditions parameter values were significantly different in certain intervals. In particular, low-water availability significantly reduced survival probability (parameter θ in the NM; likelihood profile; $P < 0.05$) for both oaks in the first interval ($T_0 \rightarrow T_I$), for Q. pyrenaica in the second ($T_I \rightarrow T_{II}$) and fourth intervals ($T_{III} \rightarrow T_{IV}$) and reduced the asymptotic survival at high irradiance in the MM model (parameter α_0; likelihood profile; $P < 0.05$) for Q. robur in the third interval ($T_{II} \rightarrow T_{III}$).

4. Discussion

4.1. Variation in species responses

Our study shows species-specific responses in seedling survival across time intervals with species differing both in the type of functional response and in the relative performance at a given part of the irradiance gradient. Q. robur, a light demanding species in most comparative studies (Van Hees, 1997; Valladares et al., 2002), and Q. pyrenaica were the two most shade tolerant species in our study. Under well-watered conditions, seedlings of Q. pyrenaica were more tolerant of shade than seedlings of Q. robur as the former followed a constant probability of survival along the irradiance gradient (NM) on all four time intervals, while the latter followed a light dependence model in the third interval. Also, under conditions of low-water availability, seedlings of Q. robur exhibited irradiance dependency (i.e. MM model) throughout the whole experiment ($T_0 \rightarrow T_{IV}$), while Q. pyrenaica did not and followed the same NM model as under well-watered conditions. Survival patterns of seed-
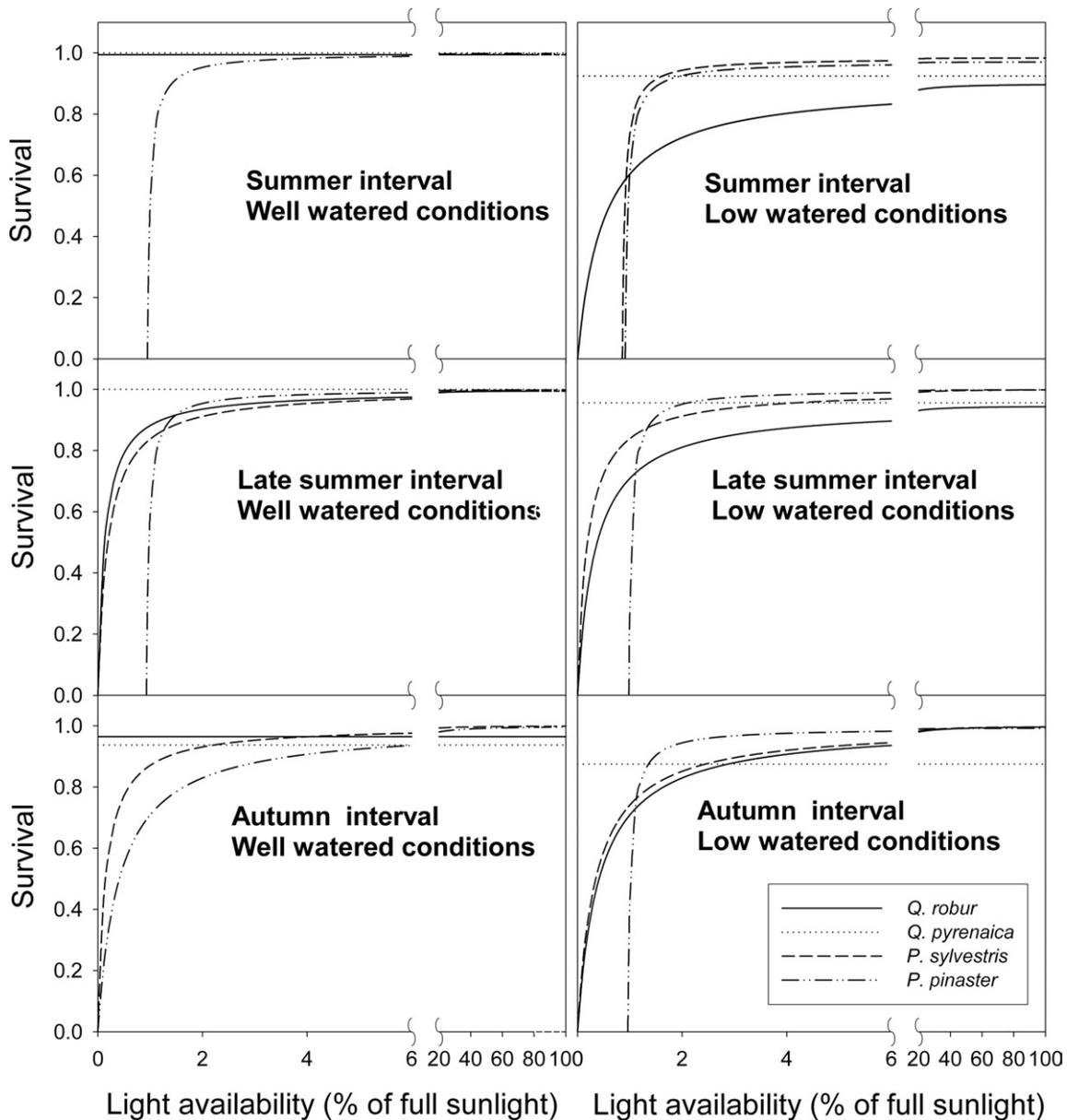
Fig. 2 – Models resulting in the best fit for seedling survival along the irradiance gradient for each time interval and water availability level. Lengths of the intervals are 29, 24 and 26 days for summer, late summer and autumn intervals, respectively, N = 44.

lings of *P. pinaster* exhibited irradiance dependence for three intervals under the well-watered treatment, as opposed to two intervals for *P. sylvestris*, suggesting that the latter is more tolerant of shade.

Patterns of survival of seedlings found in this study are consistent with forestry classifications of shade tolerance developed for the Iberian Peninsula according to which *P. pinaster* is a light demanding species and *P. sylvestris* is a shade tolerant species in Mediterranean regions where stand regeneration is enhanced by partial light suppression (Ruiz de la Torre, 2001). In Central Europe, *P. sylvestris* is classified as a light demanding species. The higher irradiance experienced by plants in Mediterranean environments can be particularly harmful since it co-occur with drought and

heat, exerting a negative impact not only on plant ecophysiological performance (Retana et al., 1999; Valladares et al., 2005) but also on survival, as seen in this study. This fact may partially explain differences in shade tolerance between classifications obtained in Central Europe and sunnier and warmer environments as studied here.

Variation in survival rates and lack of response to irradiance observed in oak species can be also the result of ontogenetic changes in plant performance (Cavender-Bares and Bazzaz, 2000). Ontogeny can be addressed at two different scales, the long-term ontogenetic shift between juvenile and adult trees, and the short-term shifts observed during the first year of growth, where the influence of seed reserves are particularly conspicuous in large-seeded species (Sones-

son, 1994; Fenner and Kitajima, 1999). Thus notable seed size differences among oaks and pines (i.e. 3.6, 4.5, 0.007, 0.045 g for mean seed mass of *Q. robur*, *Q. pyrenaica*, *P. sylvestris* and *P. pinaster*, respectively; Catalán Bachiller, 1993) could partially explain the greater sensitivity of pines to shade during the first dry season.

4.2. Inter-specific comparison: implications for stand dynamics and species coexistence

According to Poorter and Arets (2003), niche differentiation through resource partitioning (e.g. light) requires in addition to the existence of a resource gradient and a differential species distribution along the gradient, the existence of a trade-off in species performance. We found that large species (in terms of seedling biomass) with higher survival in low irradiance (oaks) exhibited lower survival at high irradiance and vice-versa (see parameter α_0 versus θ for high light performance and type of response, MM or NZ versus NM for shade tolerance, Tables 2 and 3 and Fig. 3). Differences in species survival under high light were slight but would be consistent with a trade-off between low/high light survival. Further experimental and field comparative studies are required in order to test the existence of a general sun-shade trade-off. Trade-offs among performance at high and low irradiance have been reported in leaf-level ecophysiological traits (see Reich et al., 2003 and references therein) and whole plant growth (Lorimer, 1981; Givnish, 1988; Popma and Bongers, 1988) and less so with respect to mortality (but see Pacala et al., 1996) even though the trade-off is present in some of these studies (see for example Lin et al., 2002; Kobe et al., 1995). A possible reason for the lack of reporting of sun-shade trade-off in survival is due to the fact that most of the previous studies have been carried out under relatively low irradiance (lower than the present study). In light-limited tropical and mesic temperate forests, increasing irradiance levels always improved plant performance (Canham et al., 1990; Walters and Reich, 1996; Agyeman et al., 1999; Kitajima, 2002; Valladares, 2003), but maximal irradiance levels considered were in general lower than those in our experiment and

thus negative effects of excessive radiation could have been overlooked.

Effects of low-water availability on seedling survival were species-specific both at low and high irradiance. *Pinus* species were found to be more drought tolerant than oaks. Such differences in drought tolerance may be a consequence of different physiological and morphological adaptations (see for instance Abrams, 1991; Reich et al., 1992; Caspersen and Kobe, 2001). At an intra-specific level, Sack and Grubb (2002, see also Sack, 2004) have reviewed five general models of functional responses to combined shade and drought. The three most contrasted hypotheses of those discussed by Sack and Grubb (2002) are considered here. Drought will be increasingly harmful under shadier conditions because of conflicts in the amount of resources that can be simultaneously allocated to cope with both above- and below-ground limitations (trade-off hypothesis, Smith and Huston, 1989; Kubiske et al., 1996). Alternatively, the impact of drought decreases under increasing shade as part of a facilitation process by which the negative effects of irradiance suppression are offset by benefits to plant water status (Callaway, 1995; Flores and Jurado, 2003; Prider and Facelli, 2004). Finally, it has been suggested that drought has a fixed proportional impact across the irradiance gradient (Sack and Grubb, 2002; Sack, 2004). Our results showed a similar impact of low-water availability on either low or high irradiance for *Q. pyrenaica* with decreasing survival at both low and high irradiance in agreement with the orthogonal hypothesis. However low-water availability mainly impacted on low irradiance and less so on high irradiance for *Q. robur*. These findings suggest that the impact of drought on survival along an irradiance gradient is species dependent. However, further research for a wider range of ecophysiological variables is needed in order to unravel the complex interactive effects of irradiance and water availability on seedlings responses along gradients of these factors.

We did not find evidence of conclusive differences in drought tolerance among *Pinus* species. This can be due to the range of water stress considered in our study which was
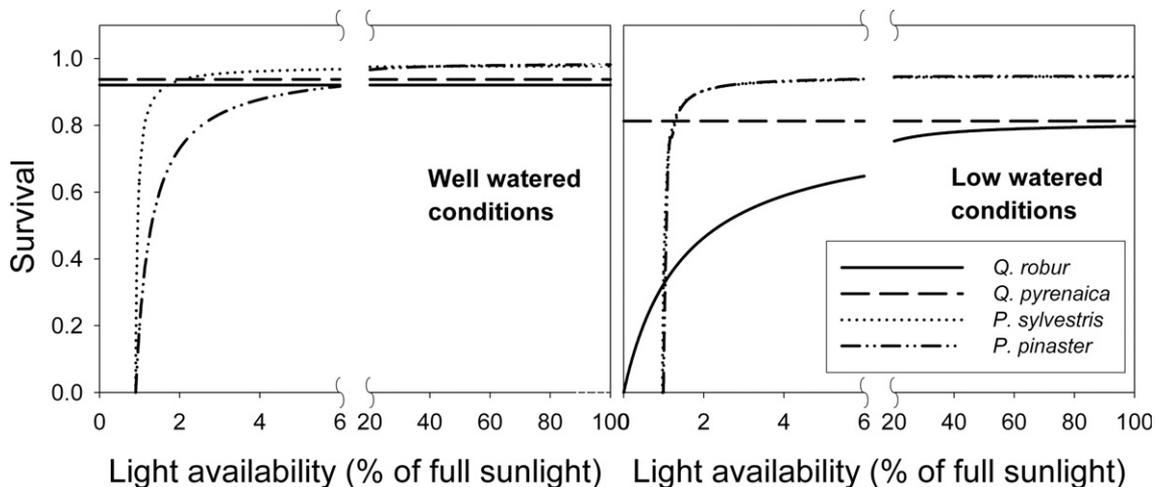
Fig. 3 – Comparison between survival curves evaluated at the end of the experiment ($T_0 \rightarrow T_{IV}$) for each species in both well-watered and low-water conditions. Length of the considered interval = 109 days, N = 44.

not broad enough as to induce a differential response across pines.

Interestingly, higher mortality in low irradiance compared to high irradiance for water-stressed seedlings has previously been found for other species (Vance and Zaerr, 1991; Sack, 2004). Nevertheless, those studies assessed the impact of strong drought in different irradiances opposite to this study where deep shade but moderate drought were considered.

The interaction between irradiance and water availability and its effect on seedling survival can have a dramatic impact on species coexistence and forest dynamics in this region (Zavala and Zea, 2004). Current empirical classifications of shade tolerance are based on an amalgam of intuition and subjective observations which include a range of tree sizes and site conditions. In heterogeneous Mediterranean forests where atmospheric water demand or patterns of water availability can change at very short spatial scales (e.g. because of slope aspect, Gómez-Aparicio et al., 2004), species responses to irradiance cannot be easily grouped into categories. Rather the formulation of flexible statistical models that allow characterizing a continuum of plant functional responses comparable across sites is required (Pacala et al., 1994; Kobe, 1999). As drought occurs with increasing frequency and severity in forest worldwide (Fearnside, 1995; Karl et al., 1995; Peñuelas et al., 1998) with already visible impacts on forest species dominance and on ecotones and transition zones (Peñuelas and Boada, 2003) it is critical that we attain a sound understanding of the interactive effects of irradiance and water availability on survival and growth of seedlings and juvenile plants. Our study highlights the need to improve the connection between existing theoretical models (Holmgren et al., 1997) and experimental data (Holmgren, 2000; Sack and Grubb, 2002). Increasing both the number of species and the range of resource variation considered is needed before a mechanistic understanding of stand dynamics in this region is attained. The development of seedling survival models in response to the availability of different resources provide an accurate way of determining inter-specific differences at the optimum range for seedling performance within co-occurring resource gradients. Consequently, these kinds of models are a promising tool that can be used in a practical sense to reduce seedling mortality in reforestation practices.

Acknowledgments

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