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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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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.

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 interspecific 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-

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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 significance 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).