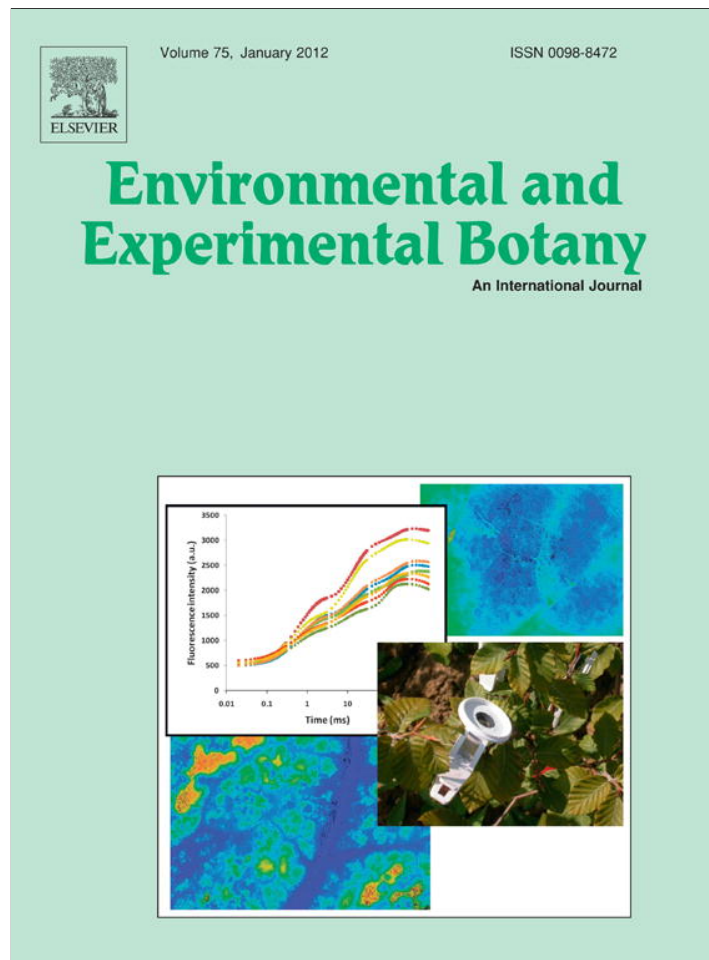


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Evidence for plant traits driving specific drought resistance. A community field experiment

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ABSTRACT

Drought is known to be a major bottleneck for woody-community recruitment. The species-specific resistance to drought and factors involved in its variation are of special interest to forecast community fate. We performed an experiment under natural field conditions from winter 2006 to end summer 2008 to investigate the structural responses of woody saplings to nine combinations of light (three habitats differing in plant cover: forest, shrubland, and open) and water (three climate scenarios: drier, current and wetter summers). Our working hypothesis is that plant strategies to cope with drought are determined by habitat characteristics and/or variation of plant traits, and that these different strategies may determine community composition and dynamics. Eight woody species with different life forms and successional stages (trees, mid-successional shrubs, and pioneer shrubs) were selected for the comparison, including therefore species representative of the entire woody community. We explored drought resistance at the population level (D_S), the relations of the different morphological traits to D_S , and the potential importance for plants of inter-specific trade-offs. D_S ranged from 0% to 99% for the different species, depending on the habitat. Some structural traits were found to be related to D_S : positively with total biomass and leaf mass ratio (LMR) and negatively with leaf area-root mass ratio (LARMR). Contrary to previous studies, the present work revealed no evidence of trade-offs, such as survival in forest vs. growth in open, or growth in forest vs. growth in open. Accordingly, some species with low D_S values (*Acer opalus* and *Pinus sylvestris*) would be threatened under the future climate conditions, while species having structural characteristics to increase their resistance under expected dry years in coming decades (i.e., high LMR and total biomass or low LARMR, such as *Quercus ilex* and the shrub *Cytisus scoparius*) might enhance their recruitment probabilities. Thus, species-specific plant traits, and their effect on D_S , may filter future community assemblages.

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1. Introduction

Species-specific differences in the ability to survive drought may be a major factor influencing plant-community composition (Engelbrecht and Kursar, 2003). With declining amounts and increasing variability of precipitation expected for the coming decades throughout large areas of the planet (Houghton et al., 2001), drought may exert an even stronger control of species distribution at both local and regional scale (Engelbrecht et al., 2007). Thus, a proper study of the specific variations in

drought resistance and the factors involved in its determination is of special interest in order to forecast future plant-community changes.

At the community level, species from different successional stages (i.e., pioneer shrubs, successional shrubs, or trees; *sensu* Thompson, 2005) show different tolerance to drought (Engelbrecht and Kursar, 2003; Sack, 2004), and therefore are expected to respond in different ways to climate shifts. Differences in the drought resistance may sort species within the community (*sensu* Herrera, 1992), thereby driving community spatio-temporal dynamics. At the species level, changes in habitat characteristics within an ecosystem may alter growth traits such as plant size, specific leaf area or biomass-allocation patterns (Lloret et al., 1999; Poorter and Hayashida, 2000; Poorter et al., 2009), resulting ultimately in a shift in drought resistance. In this context, our working hypothesis is that plant strategies to cope with drought are determined by habitat characteristics and/or variation of plant traits, and that these different strategies may determine community composition and dynamics.

Abbreviations: D_S , Drought resistance in terms of survival; GSF, Global site factor; LAR, Leaf area ratio; LARMR, Leaf area root mass ratio; LMR, Leaf mass ratio; RMR, Root mass ratio; SLA, Specific leaf area; SMR, Stem mass ratio; SSL, Specific stem length.

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Plant sensitivity to drought may be evaluated using different proxies of plant physiological status, such as water potential, stomatal conductance, or chlorophyll fluorescence (Gómez-Aparicio et al., 2006; Quero et al., 2006, 2011). However, few studies have demonstrated that a single physiological variable correlates with plant survival (Tyree et al., 2003). Therefore, an integrative measure of drought resistance at the population level such as the one described by Engelbrecht and Kursar (2003), which is based on species-specific survival under contrasting water availabilities, provides a powerful tool to examine inter-specific responses to drought.

Although specific drought responses in terms of survival and growth vary along a continuous gradient, strategies for coping with drought can be classified as: (1) little effect on both growth and survival; (2) little effect on survival, but strong effect on growth; (3) strong effect on survival, with the surviving individuals showing a low to moderate growth reduction (Engelbrecht and Kursar, 2003). These responses have resulted in some cases in different trade-offs previously reported in literature for other plant communities and approaches (Sack, 2004; Sánchez-Gómez et al., 2006). Most studies relating growth and survival have been developed in tropical and temperate forests (Kitajima, 1994; Pacala et al., 1996; Kobe, 1999; Dalling and Hubbell, 2002; Seiwa, 2007), but information remains scant concerning this relationship in Mediterranean areas, especially under field conditions (but see Zavala et al., 2000).

The common way of analysing the relationships between light and water availability to plant performance is under controlled conditions in pot experiments (Quero et al., 2006; Sánchez-Gómez et al., 2006). Natural regeneration, however, takes place in a much more complex (real) scenario, where many biotic and abiotic factors act simultaneously and interactively (Ibáñez and Schupp, 2001; Gómez, 2004). Although studies under controlled conditions present clear research advantages, measured plant traits not always reflect the range of variation when subjected to natural conditions (Karel and Julian, 2008). Thus, only by field studies encompassing the natural light-variability range, can plants express the phenotypic reality that is not always matched under the controlled greenhouse conditions. In this sense, we have designed an experiment under natural field conditions to investigate the structural responses of woody saplings to nine combinations of light (three habitats) and water (three climate scenarios) availability. The use of saplings offers additional advantages with respect to the use of adult individuals as the high sapling sensitivity to abiotic conditions, due to their limited root system and quicker responses to environmental changes, representing a good study subject to explore species-specific effects of drought. Eight woody species with different life forms and successional stages (trees, successional shrubs, and pioneer shrubs) were selected for the comparison, including therefore species representative of the entire woody community. A complete set of plant traits, both at above-ground and below-ground, were measured. The specific questions posed were: (1) What is the drought resistance of saplings from species representative of the main successional strategies in Mediterranean mountains across different habitats? (2) Which morphological traits increase drought resistance in the different successional strategies? (3) Is there any evidence of trade-offs in response to different light and water availability in Mediterranean mountains?

2. Materials and methods

2.1. Study area and species

The study was conducted within the Sierra Nevada National Park (37°05' N, 3°28' W, Granada, SE Spain), at an elevation of c. 1650 m

a.s.l. between December 2006 and September 2008. This mountain area has a continental Mediterranean climate, with cold and snowy winters and hot, dry summers. The mean minimum temperature in the coldest month (January) is -1.1°C , and the mean maximum of the hottest month (July) is 29.2°C . Rainfall reaches 811 mm yr^{-1} , mostly during spring and autumn (means 1990–2008). The vegetation in the area is composed of patches under different successional stages, with forest stands dominated by Scots and Black pines (*Pinus sylvestris* L. and *P. nigra* Arnold.) and oaks (*Quercus ilex* L.) mixed with shrublands, and open areas. The experiment was conducted inside a natural area of 12.4 ha fenced since 1986 to prevent browsing by ungulates.

We selected eight woody species from a diverse successional range from pioneer shrubs to trees: *Salvia lavandulifolia* Vahl., *Cytisus scoparius* L., *Berberis vulgaris* L., *Crataegus monogyna* Jacq., *Sorbus aria* L., *Acer opalus* Mill., *Pinus sylvestris* L. and *Quercus ilex* L. (hereafter these plants will be referred to by their genus names). More information on species characteristics can be found in Table 1. All of these plants occur naturally in the area and are representative of the three main successional stages: pioneers, mid-successional, and late-successional. Seeds and acorns from these species were collected on the surrounding area during 2006 fruiting period (September–December). Then, they were visually inspected to reject clearly aborted or depredated ones and stored at 4°C until the sowing.

2.2. Experimental design

To test the effect of light and water availability on growth and morphological characteristics of woody saplings, we performed a fully factorial field experiment crossing these main factors, each with three levels. For the light treatment, we selected the three main Mediterranean mountain habitats where seedling emergence naturally occurs (Matías et al., 2011a), ranging from high to low light availability: open areas, under shrub canopy, and under tree canopy. Hereafter, these habitats will be called *open*, *shrubland*, and *forest*, respectively. For the water-availability treatment, we selected three levels based on different climate scenarios: (1) dry summer, based on the SRES A-2 model by Intergovernmental Panel on Climate Change (IPCC, 2007), where a reduction on summer rainfall of 30% is predicted for Mediterranean areas. We built rain exclusion shelters (Yahdjian and Sala, 2002) formed by a $2\text{ m} \times 2\text{ m}$ metal frame supporting V-shaped clear methacrylate bands without UV filter (Barlocast®; Faberplast S.L., Madrid), covering 35% of the surface, and intercepting the same percentage of natural water supply by rain. A ditch 20 cm deep was excavated along the entire shelter to intercept runoff water. Rainout shelters were placed from April to September to simulate drier and longer summers. (2) Rainy summer, to simulate the rainy summers that occasionally occur in Mediterranean mountains (Matías et al., 2011b), we placed $2\text{ m} \times 2\text{ m}$ squares on the soil with a watering system composed of 4 sprinklers at the corners. Each week, from mid June to end September, we applied a water pulse of 12 l m^{-2} , simulating a summer storm. If a natural storm occurred within the period of one week, the irrigation pulse was not added. The total water added during the summer was 180 l, equivalent to the mean summer rainfall of the five mildest summers of the 1902–2008 series in the study area (Matías et al., 2011b). (3) Current conditions, natural rainy conditions throughout the experiment. We placed $2\text{ m} \times 2\text{ m}$ squares without water addition or exclusion, acting as control for the experiment. Hereafter, these climate scenarios will be called *dry*, *wet*, and *control* scenarios, respectively. Eight replicated plots of each climate scenario were randomly placed in each of the three habitats, for a total of 72 plots (8 replicates \times 3 climate scenarios \times 3 habitats). Precipitation during treatment applications (April to September) was 366 l m^{-2} and 375 l m^{-2} in 2007 and

Table 1

Summary of the species studied: life form (T, tree; Sh, shrub; B, broom; Sc, scrub), foliar longevity (D, deciduous; E, evergreen), strategy (LS, late-successional; MS, mid-successional; P, pioneer), origin (SM, sub-Mediterranean; BA, Boreal-Alpine; M, Mediterranean, following Blanco et al., 2005). Seed mass indicates the mean seed-mass value ($n = 360$ for *Quercus*, $n = 100$ for the rest). Sowed seeds represent the number of seeds sowed from each species per plot.

Species	Family	Life form	Foliar longevity	Strategy	Origin	Seed mass	Sowed seeds
<i>Acer opalus</i>	Aceraceae	T	D	LS	SM	0.046	15
<i>Pinus sylvestris</i>	Pinaceae	T	E	LS	BA	0.012	15
<i>Sorbus aria</i>	Rosaceae	T	D	LS	SM	0.036	10
<i>Quercus ilex</i>	Fagaceae	T	E	LS	M	4.480	5
<i>Crataegus monogyna</i>	Rosaceae	Sh	D	MS	M	0.079	15
<i>Berberis vulgaris</i>	Berberidaceae	Sh	D	MS	M	0.018	15
<i>Cytisus scoparius</i>	Fabaceae	B	E	P	M	0.011	15
<i>Salvia lavandulifolia</i>	Lamiaceae	Sc	E	P	M	0.005	15

2008, respectively (above the mean value of the 1990–2008 series). Thus, precipitation in the dry-summer scenario was 2381 m^{-2} and 2431 m^{-2} in 2007 and 2008, respectively, and 5461 m^{-2} and 5551 m^{-2} in the wet-summer scenario.

In each plot, seeds of the eight species studied were sown inside individualised cages ($1\text{ cm} \times 1\text{ cm}$ wire mesh width) to avoid predation by small mammals. The number of seeds sown differed for each species depending on seed mass and germination rates, checked in a previous experiment (Mendoza et al., 2009a) as ranging from 5 to 15 (Table 1). The sowing was performed in December 2006, and seeds remained on the soil the entire winter period, undergoing natural cold stratification in the field. Light availability was measured in all plots by hemispherical photography (Valladares and Guzmán, 2006), estimating the global site factor (GSF), representing the total amount of light, ranging from 0 (light absence) to 1 (100% light availability). In the 72 study plots, the water content of the soil from the top 20 cm was measured monthly by the time-domain reflectometry method (TDR-100, Spectrum Technologies Inc., Plainfield, IL), sampling all study plots by two perpendicular transects and recording the volumetric water content every 0.5 m ($N = 9$ per plot). All measures were made systematically after two days from irrigation events (Matías et al., 2012 for more details).

On September 2008, after two complete growing seasons, all surviving saplings were harvested. The whole plants were extracted by excavating the whole root system with a pneumatic hammer. The roots were carefully washed to remove soil remains; the plants were placed in individualised plastic bags with a moist atmosphere to maintain leaf hydration, and kept under colder conditions to the lab, where structural measures were made. Stem and root length as well as leaf area were determined in fresh. We measured the maximum root length of the plant, as recommended by Poorter (1999). Leaf area was calculated for the whole plant, by scanning all leaves and processing the images with an image-analysis software (Image Pro-Plus v 4.5, Media Cybernetic Inc., Silver Spring, MD, USA). Divided into leaves, stem, and roots, the plants were oven dried at 70°C for at least 72 h, and weighed. The primary data provided the following variables: root mass ratio (RMR; root mass/total plant mass, g g^{-1}), leaf mass ratio (LMR; leaf mass/total plant mass, g g^{-1}), stem mass ratio (SMR; stem mass/total plant mass, g g^{-1}), specific leaf area (SLA; total leaf area/total leaf mass, $\text{m}^2\text{ kg}^{-1}$), leaf area ratio (LAR; total leaf area/total plant mass, $\text{m}^2\text{ kg}^{-1}$), leaf area root mass ratio (LARMR; total leaf area/root mass, $\text{m}^2\text{ kg}^{-1}$), and specific stem length (SSL; stem length/stem mass, cm g^{-1}). These variables refer, respectively, to biomass allocation (RMR, SMR, LMR), leaf display (SLA, LAR), the balance between investment in light intercepting organs vs. water and nutrient uptake organs (LARMR), and the efficiency of biomass investment for height gain (SSL) (Poorter, 1999).

2.3. Data analysis

Soil volumetric water content and light availability (expressed as GSF) were analysed among habitats and climate scenarios by a

repeated-measures ANOVA and factorial ANOVA, respectively. To avoid pseudoreplication, we calculated the mean value for the different variables (total biomass, RMR, SMR, LMR, SLA, LAR, LARMR, and SSL) from all saplings surviving in each plot per species. These values were used to test the effects of habitats and climate scenarios on each morphological variable and species by linear models (R 2.9.1, R Development Core Team, 2009). All variables were transformed to their natural logarithms before analysis following Poorter and Garnier (1996) recommendations.

Also, we calculated the drought resistance of each species growing in the different habitats in terms of survival (D_S) as the percentage of survival in the dry scenario relative to the wet scenario:

$$D_S = \left(\frac{S_D}{S_W} \right) \times 100$$

where S_D and S_W are the number of saplings surviving at the end of the second growing season relative to the number of emerged saplings under the dry and wet scenarios, respectively (Engelbrecht and Kursar, 2003). This index was correlated for each species and habitat with morphological variables to assess their importance in drought resistance. Similarly, survival in forest vs. growth in open, and growth in forest vs. growth in open were related by a Spearman-rank correlation to check for the aforementioned trade-offs. Results throughout this paper are given as mean \pm SE.

3. Results

3.1. Efficiency of water and light treatments

Light availability (expressed as GSF) ranged from 0.10 to 0.91, representing almost the entire range of natural-light availability in Mediterranean areas (Valladares et al., 2004). Open was the habitat with the highest radiation values (0.87 ± 0.01), followed by shrubland (0.42 ± 0.02), and forest (0.22 ± 0.01). These values significantly differed between habitats ($F_{2,63} = 451.5$; $P < 0.0001$), but there were no significant differences either between climate scenarios ($F_{2,63} = 1.30$; $P = 0.28$), or in the interaction of these two factors ($F_4 = 0.36$; $P = 0.84$). Soil volumetric water content also significantly differed among habitats ($F_{2,715} = 499.7$, $P < 0.0001$; forest $15.1 \pm 0.18\%$, shrubland $14.6 \pm 0.17\%$, open $12.4 \pm 0.15\%$), and among climate scenarios ($F_{2,715} = 1214.7$, $P < 0.0001$; wet summer $16.4 \pm 0.16\%$, control $13.8 \pm 0.18\%$, dry $11.9 \pm 0.15\%$).

3.2. Drought resistance in terms of survival

Sapling survival after the second summer was higher in the wet scenario than in the dry scenario for all species, although differences appeared among functional groups and habitats. Accordingly, drought resistance (D_S) ranged from 0% for *Pinus* in all habitats to 99% for *Cytisus* in shrubland (Fig. 1). Overall, *Quercus* and *Cytisus* were the most drought-resistant species, whereas *Acer* and especially *Pinus* were the most drought-sensitive ones. Considering

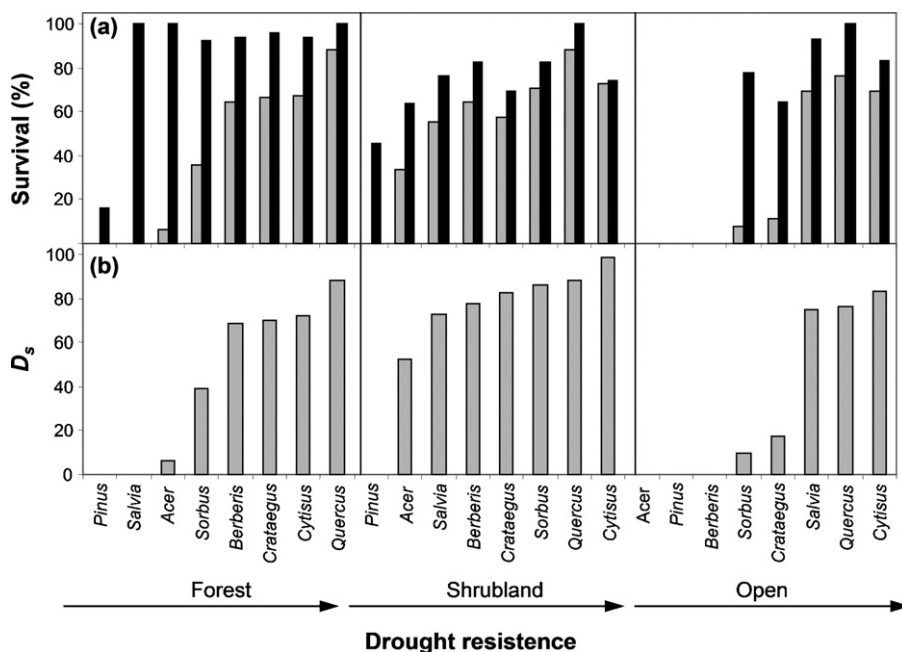


Fig. 1. (a) Survival percentage at the end of the experiment relative to the number of emerged seedlings in the irrigated (black bars) and dry (grey bars) treatments. (b) Drought resistance index in terms of survival (D_5 ; unitless) calculated as survival in the dry-summer scenario relative to the wet-summer scenario ($D_5 = S_D/S_W \times 100$) in each habitat. Species are sorted by increasing drought resistance in terms of survival. The D_5 index is represented by black bars for trees, grey bars for mid-successional shrubs, and white bars for pioneer shrubs.

successional strategies, pioneer shrubs showed a high D_5 in all habitats, except *Salvia* in forest. Mid-successional shrubs also had a high D_5 in forest and shrubland habitats but low in open. For tree species, *Pinus* and *Acer* registered a low D_5 in all habitats; *Sorbus* had the highest D_5 in shrubland, followed by forest and open; and *Quercus* had a similar high D_5 across habitats.

3.3. Effect of habitat and climate scenarios on sapling morphological traits in relation to drought resistance

Habitat and climate scenario affected morphological traits differently across species and functional groups. Among morphological traits, some, such as RMR, SLA, LAR or LARMR were affected mainly by habitat for most species, whereas the other variables (total biomass, LMR, SMR, SSL) were also affected by climate scenario (Table S1). Some of the structural traits explained D_5 among species and within habitat. D_5 was positively related to total biomass and LMR in open habitat: plants with higher total biomass and LMR had also higher D_5 in open habitat (Fig. 2). Furthermore, LARMR negatively contributed to D_5 in shrubland: plants with higher leaf area per unit of root mass had lower drought resistance.

3.4. Interspecific trade-offs

No relation was found between survival in the shadiest habitat (forest) and growth in the open habitat among our set of species in any of the climate scenarios (Fig. 3a). Thus, species with high growth in the open habitat did not have low survival in forest or vice versa. Likewise, there was no relationship between absolute growth in forest and absolute growth in the open (Spearman's rank correlations non-significant in all climate scenarios; Fig. 3b).

4. Discussion

Many studies have evidenced that the consequences of drought can be assessed reliably only in terms of survival rather than growth

performance under field and greenhouse conditions (Engelbrecht and Kursar, 2003; Tyree et al., 2003). However, no studies available have explicitly analysed to date species-specific drought resistance from different woody functional groups to different habitat canopies. Our field experiment demonstrated for the first time that D_5 varies across species and habitats, determined by total biomass, LMR, and LARMR, and that there is no evidence of any inter-specific trade-offs in this woody community.

4.1. Specific drought resistance under different habitats

Species from different successional strategies presented different D_5 , this being modulated by habitat structure. By groups, pioneer shrubs showed high D_5 in general terms, although habitat conditions strongly affected the resistance of the pioneer *Salvia*, which was very low under the forest canopy but very high in the open habitat. The other pioneer species (*Cytisus*) presented high D_5 in all habitats, being the highest in shrubland and open. For both pioneer species, we found that higher canopies reduced D_5 , confirming therefore their necessities of illuminated places and their pioneer status. Mid-successional shrubs presented very similar D_5 values (around 75%) when a woody canopy was present, but had low resistance in the open, especially *Berberis*. This may indicate the need of the prior establishment of drought-tolerant species (pioneers shrubs) to provide microclimatic conditions conducive to mid-successional success (Broncano et al., 1998; Rodá et al., 1999). Regarding tree species, we found high D_5 variability among them. *Pinus* survived only in the wet climate scenario in shaded habitats ($D_5 = 0$). This species is able to recruit new individuals only during the milder years, as indicated in previous studies in the same area (Castro et al., 2004; Mendoza et al., 2009a). *Acer* presented high D_5 only in shrubland, whereas values were very low in the other habitats. For establishment, *Acer* saplings need the protection of nurse species (Gómez-Aparicio et al., 2005; Quero et al., 2008). *Sorbus* was able to establish in any habitat, but showed the highest D_5 in shrubland. As occurred with *Acer*, *Sorbus* saplings establish better under shrub canopies (Mendoza et al., 2009b), but were also able

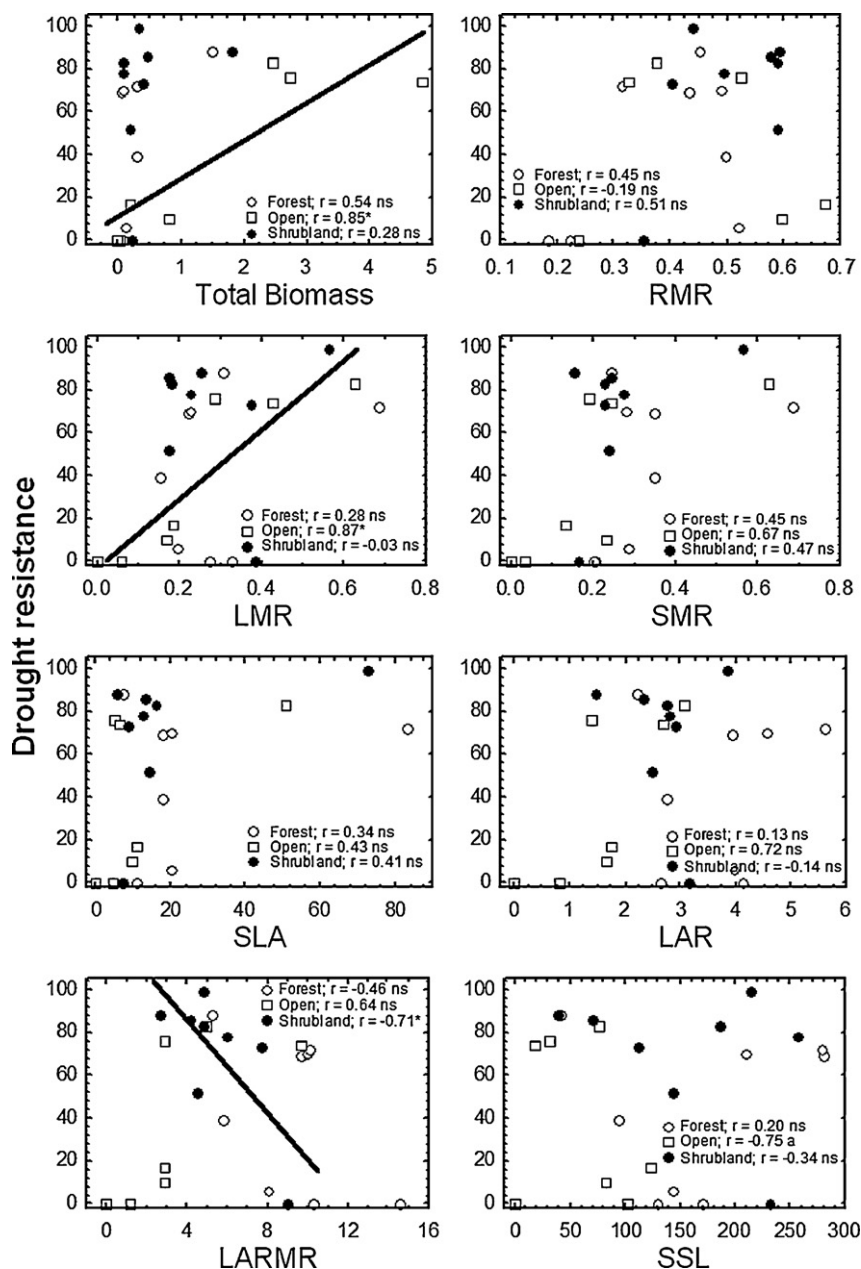


Fig. 2. Relations between drought resistance and seedling morphological traits: (a) total biomass (expressed in g); (b) RMR, root mass ratio (g g^{-1}); (c) LMR, leaf mass ratio (g g^{-1}); (d) SMR, stem mass ratio (g g^{-1}); (e) SLA, specific leaf area ($\text{m}^2 \text{kg}^{-1}$); (f) LAR, leaf area ratio ($\text{m}^2 \text{kg}^{-1}$); (g) LARMR, leaf area root mass ratio ($\text{m}^2 \text{kg}^{-1}$); and (h) SSL, specific stem length (cm g^{-1}). White circles represent species growing in forest, white squares in open, and black circles in shrubland. Climate scenarios are pooled. r-values and significance ($P \leq 0.05$; $0.01 < P < 0.05$) are indicated within the different panels. Significant Spearman's correlations are represented within habitats.

to survive in the open. *Quercus* was, by far, the tree species with the highest D_5 in all habitats. Surprisingly, the two species with the highest drought resistance, regardless of the canopy, were *Cytisus* and *Quercus*, a pioneer shrub and tree, respectively. These two species show different strategies to cope with drought: *Cytisus* may be considered a drought avoider (*sensu* Valladares et al., 2008), since their leaves are shed in summer to reduce transpiration while maintaining stem photosynthetic function. On the other hand, *Quercus* keep most of their leaves in the tree crown during the summer, and may be considered a drought-resistant species, presenting different mechanisms to cope with drought such as low specific leaf area, embolism resistance, or an isohydric strategy (Quero et al., 2011). Thus, although both species share mechanisms to uptake carbon during the summer drought (i.e., less water lost from the leaves),

they can be ordered along an avoider-resistant axis, from *Cytisus* to *Quercus*.

4.2. Structural traits and drought resistance

Overall, we found that D_5 was partially explained by some structural traits, although this relation did not appear in all habitats. Total biomass as well as LMR, were positively related to D_5 , but only in the open habitat. Plants with the greatest biomass proved more resistant to drought in terms of survival. Although a different proportion in roots did not explain the D_5 values (Fig. 2), higher plant biomass may allow either the uptake of water from deeper soil profiles or higher reserve storage (Lloret et al., 1999; Paula and Ojeda, 2009). Regarding LMR, the positive relationship with D_5

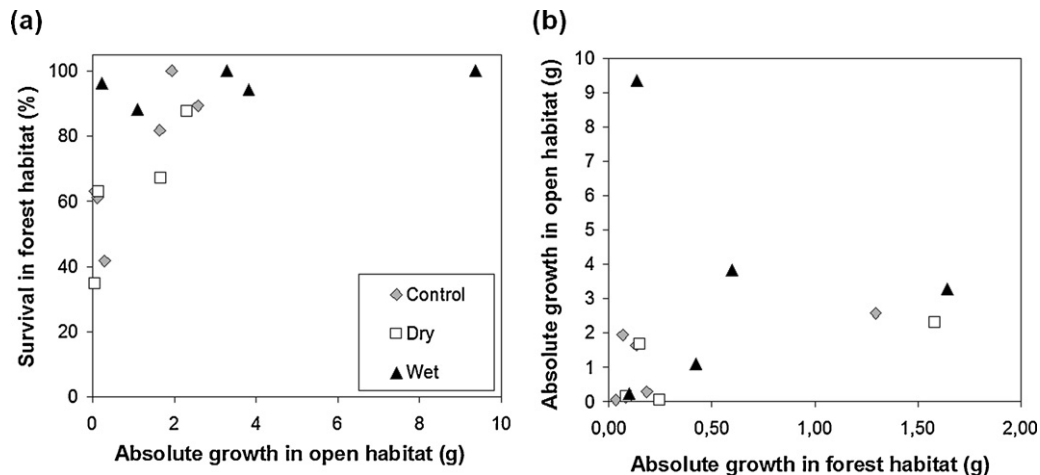


Fig. 3. (a) Relations between survival in forest habitat vs. absolute growth in open (expressed as final dry mass at the end of the experiment), and (b) between absolute growth in open vs. absolute growth in forest by climate scenarios (control: grey diamonds; dry: open squares; wet: black triangles). Each point represents the mean value by species. Only those species with at least one surviving individual are included. Spearman's R correlations were non-significant in all cases.

could be explained as a consequence of the highest leafing intensity (i.e., leaf number per shoot volume) in open habitat (authors' personal observation). Higher leafing intensity imply lower leaf size (Milla, 2009), which can be a mechanism for heat dissipation by increasing the ratio of leaf perimeter to surface area (Vogel, 1968). The absence of any relation in the two habitats covered by plants (forest or shrubland) may be induced by a growth limitation (but no survival limitation). In these habitats, saplings may be partially limited by light, being unable to adapt their morphology efficiently enough to bolster their drought resistance, and expressing therefore these relations only in the habitat where light is not a limiting factor (Aranda et al., 2005). We also found a significant relation between LARMR and D_5 in shrubland, indicating that species with higher investment in light-intercepting organs in relation to water and nutrient-uptake organs are less able to cope with drought. An increase in leaf area is generally a response to lower light availability (Ellsworth and Reich, 1992, 1993; Niinemets and Kull, 1994; Niinemets and Tenhunen, 1997) at the expense of higher root development (Smith and Huston, 1989). Lower LARMR promotes higher efficiency in water uptake, and may be a competitive advantage under conditions where other factors limit growth and survival more than does light (Walters and Reich, 1996).

4.3. Interspecific trade-offs

Contrary to the general pattern found in tropical (Kitajima, 1994; Kobe, 1999; Dalling and Hubbell, 2002) or temperate environments (Kobe et al., 1995; Pacala et al., 1996; Seiwa, 2007), where trade-offs seem to be widespread, we found no evidence of such relationships for the Mediterranean species studied. Only a few studies explicitly analyse relations between growth and survival in Mediterranean woody species, and the overall sign is still unclear. The lack of trade-off found under field conditions in our experiment contrasts with the results reported by Sánchez-Gómez et al. (2006) in a pot experiment, also with Mediterranean trees and shrubs. They found a negative relationship between relative diameter growth and survival under very low-light intensities, but our results do not support this pattern under field conditions. These differences between field and greenhouse experiments might be related to the more complex and realistic scenario under field conditions as well as to the use of a different growth indicator, such as the final biomass. The few field studies analysing this trade-off in Mediterranean woody species have found either no

evidence of such a trade-off (Zavala et al., 2000), or weak evidence that disappears when phylogenetic effects are taken into account (Martinez-Vilalta et al., 2010). Thus, the findings of the present study indicate that no trade-offs appear in Mediterranean environments contrary to tropical or temperate forests.

4.4. Conclusions

In accordance with the results presented in this paper, some tree species with low D_5 as *P. sylvestris* or *A. opalus* might undergo a slow-down or even a halt in recruitment under the future climate conditions. These species-specific responses to climate variations might result in community changes such as biodiversity loss or assemblage alterations (Lloret et al., 2004; Thuiller et al., 2005). On the contrary, species having structural characteristics that strengthen their resistance to expected dry years in coming decades (i.e., high plant biomass, LMR or low LARMR) as *Q. ilex* might enhance their recruitment probabilities. In this sense, our study suggests that a species sorting within the community (*sensu* Herrera, 1992) mediated by structural traits may explain changes in species and functional-group dominance, and may ultimately determine the community assemblage in the coming decades.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.envexpbot.2012.03.002](https://doi.org/10.1016/j.envexpbot.2012.03.002).

References

- Aranda, I., Castro, L., Pardos, M., Gil, L., Pardos, J.A., 2005. Effects of the interaction between drought and shade on water relations, gas exchange and morphological traits in cork oak (*Quercus suber* L.) seedlings. *For. Ecol. Manage.* 210, 117–129.
- Blanco, E., Costa, M., Escibano, R., 2005. Los bosques ibéricos: una interpretación geobotánica. Planeta, Barcelona.
- 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.
- Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal, Mediterranean habitat. *J. Ecol.* 92, 266–277.
- Dalling, J.W., Hubbell, S.P., 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.* 90, 557–568.
- Ellsworth, D.S., Reich, P.B., 1992. Water relations and gas exchange *Acer saccharum* seedlings in contrasting natural light and water regimes. *Tree Physiol.* 10, 1–20.
- Ellsworth, D.S., Reich, P.B., 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96, 169–178.
- Engelbrecht, B.M.J., Kursar, T.A., 2003. Comparative drought-resistance of seedlings of 28 species co-occurring tropical woody plants. *Oecologia* 136, 383–393.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, 80–82.
- Gómez, J.M., 2004. Importance of burial and microhabitat on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. *Plant Ecol.* 172, 287–297.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., 2005. The regeneration status of the endangered *Acer opalus* subsp. *granatense* throughout its geographical distribution in the Iberian Peninsula. *Biol. Cons.* 121, 195–206.
- Gómez-Aparicio, L., Valladares, F., Zamora, R., 2006. Comparative response of tree saplings to light: implications for understanding inter-specific differences in nurse-plant relationship. *Tree Physiol.* 26, 947–958.
- Herrera, C.M., 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 40, 421–446.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Xiaosu, D., 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge, Cambridge University Press.
- Ibáñez, I., Schupp, E.W., 2001. Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. *Oecologia* 129, 543–550.
- IPCC, 2007. Climate Change, 2007. The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.
- Karel, M., Julian, A., 2008. Are traits measured on pot grown plants representative of those in natural communities? *J. Veg. Sci.* 19, 119–126.
- Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98, 419–428.
- Kobe, R.K., 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80, 187–201.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Lloret, F., Casanovas, C., Peñuelas, J., 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Funct. Ecol.* 13, 210–216.
- Lloret, F., Peñuelas, J., Estiarte, M., 2004. Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. *Global Change Biol.* 10, 248–258.
- Martínez-Vilalta, J., Mencuccini, M., Vayreda, J., Retana, J., 2010. Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *J. Ecol.* 98, 1462–1475.
- Matías, L., Castro, J., Zamora, R., 2011b. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. *Global Change Biol.* 17, 1646–1657.
- Matías, L., Zamora, R., Castro, J., 2011a. Repercussions of simulated climate change on the diversity of woody-recruit bank in a Mediterranean-type ecosystem. *Ecosystems* 14, 672–682.
- Matías, L., Zamora, R., Castro, J., 2012. Rare rainy events are more critical than drought intensification for woody recruitment in Mediterranean mountains: a field experiment simulating climate change. *Oecologia*, doi:10.1007/s00442-011-2234-3.
- Mendoza, I., Zamora, R., Castro, J., 2009a. A seeding experiment for testing tree-community recruitment under variable environments: Implication for forest regeneration and conservation in Mediterranean habitats. *Biol. Cons.* 142, 1491–1499.
- Mendoza, I., Gómez-Aparicio, L., Zamora, R., Matías, L., 2009b. Recruitment limitation of forest communities in a degraded Mediterranean landscape. *J. Veg. Sci.* 20, 367–376.
- Millar, R., 2009. The leafing intensity premium hypothesis tested across clades, growth forms, and altitudes. *J. Ecol.* 97, 972–983.
- Niinemets, Ü., Kull, O., 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. *For. Ecol. Manage.* 70, 1–10.
- Niinemets, Ü., Tenhunen, J.D., 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant Cell Environ.* 20, 845–866.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis, and dynamics. *Ecol. Monogr.* 66, 1–43.
- Paula, S., Ojeda, F., 2009. Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. *Botany* 87, 253–259.
- Poorter, H., Garnier, E., 1996. Plant growth analysis: an evaluation of experimental design and computational methods. *J. Trop. Bot.* 47, 1342–1353.
- Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct. Ecol.* 13, 396–410.
- Poorter, L., Hayashida, Y., 2000. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *J. Trop. Ecol.* 16, 481–498.
- Poorter, H., Niinemets, U., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytol.* 182, 565–588.
- Quero, J.L., 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.
- Quero, J.L., Gómez-Aparicio, L., Zamora, R., Maestre, F.T., 2008. Shifts in the regeneration niche of an endangered tree (*Acer opalus* ssp. *granatense*) during ontogeny: using an ecological concept for application. *Basic Appl. Ecol.* 9, 635–644.
- Quero, J.L., Sterck, F.J., Villar, R., Martínez-Vilalta, J., 2011. Water use strategies of six co-existing Mediterranean woody species during a summer drought. *Oecologia* 166, 45–57.
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rodá, F., Retana, J., Gracia, C.A., Bellot, J., 1999. Ecology of Mediterranean Evergreen Forests. Springer Verlag, Berlin.
- 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, M.A., 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.
- Seiwa, K., 2007. Trade-offs between seedling growth and survival in deciduous broadleaved trees in a temperate forest. *Ann. Bot.* 99, 537–544.
- Smith, T., Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83, 49–69.
- Thompson, J.D., 2005. Plant Evolution in the Mediterranean. Oxford University Press, Oxford.
- Thuiller, W., Lavorel, S., Araújo, M., Sykes, M.T., Prentice, C., 2005. Climate change threats to plant diversity in Europe. *Proc. Nat. Acad. Sci. U. S. A.* 102, 8245–8250.
- Tyree, M.T., Engelbrecht, B.M.J., Vargas, G., Kursar, T.A., 2003. Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiol.* 132, 1439–1447.
- Valladares, F., Aranda, I., Sánchez-Gómez, D., 2004. La luz como factor ecológico y evolutivo para las plantas y su interacción con el agua. In: Valladares, F. (Ed.), *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, EGRAF, S.A., Madrid, pp. 335–369.
- Valladares, F., Guzmán, B., 2006. Canopy structure and spatial heterogeneity of understorey light in abandoned Holm oak woodland. *Ann. For. Sci.* 63, 749–761.
- Valladares, F., Zaragoza-Castells, J., Sánchez-Gómez, D., Matesanz, S., Alonso, B., Poprtmuth, A., Delgado, A., Atkin, O.K., 2008. Is shade beneficial for Mediterranean shrubs experiencing periods of extreme drought and late-winter frosts? *Ann. Bot.* 102, 923–933.
- Vogel, S., 1968. “Sun leaves” and “shade leaves”: differences in convective heat dissipation. *Ecology* 49, 1203–1204.
- Walters, M.B., Reich, P.B., 1996. Are shade tolerance, survival and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77, 841–853.
- Yahdjian, L., Sala, O., 2002. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133, 95–101.
- 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.