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Original article

Functional traits predict drought performance and distribution of Mediterranean woody species

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ABSTRACT

Water availability is one of the key environmental factors that affect plant establishment and distribution. In many regions water availability will decline with climate change, exposing small seedlings to a greater likelihood of drought. In this study, 17 leaves, stem, root, and whole-plant traits of ten woody Mediterranean species were measured under favourable growing conditions and seedling drought survival was evaluated during a simulated dry-down episode. The aims of this study were: i) to assess drought survival of different species, ii) to analyse which functional traits predict drought survival time, and iii) to explain species distribution in the field, based on species drought survival and drought strategies. Drought survival time varied ten-fold across species, from 19 to 192 days. Across species, drought survival was positively related to the rooting depth per leaf area, i.e., the ability to acquire water from deeper soil layers while reducing transpiring leaf area. Drought survival time was negatively related to species ability to grow quickly, as indicated by high relative growth and net assimilation rates. Drought survival also explained species distribution in the field. It was found that species were sorted along a continuum, ranging between two contrasting species functional extremes based on functional traits and drought performance. One extreme consisted of acquisitive fast-growing deciduous species, with thin, soft metabolically active leaves, with high resource use and vulnerability to drought. The opposite extreme consisted of conservative slow-growing evergreen species with sclerophyllous leaves, deep roots, a low transpiring area, and low water use, resulting in high drought survival and drought tolerance. The results show that these drought strategies shape species distribution in this Mediterranean area.

1. Introduction

Water availability is a key factor for plants in many environments as reported for temperate deciduous forests (Sack, 2004), arid and semi-arid regions (Padilla and Pugnaire, 2007) and even for tropical rainforest (Engelbrecht et al., 2007). Water availability affects plant survival (Engelbrecht and Kursar, 2003; Matías et al., 2011), and therefore species distribution (Engelbrecht et al., 2007; Valladares, 2008).

Plants have developed several drought strategies to cope with these adverse drought conditions (Joffre et al., 1999; Chaves et al., 2002; Valladares, 2008). Drought-tolerant species are defined as species that are able to maintain photosynthetic activity at low levels of water availability. These are deep-rooted trees and shrubs that maintain evergreen sclerophyllous leaves during the dry summer period. In contrast, drought-avoiding species lose part of their leaves during summer, whereas geophytes and annual herbs avoid the dry season by completing their annual cycle before the start of summer drought. Coexisting species may differ therefore considerably in their tolerance and response to water limitations and in their ecophysiological traits (Ogaya and Peñuelas, 2003).

In water-stressed environments, plants face a trade-off between carbon gain and water loss (Cowan and Farquhar, 1977). When leaves close their stomata to avoid water loss due to low water availability in the soil (Zweifel et al., 2007) this also implies a decreased CO_2 uptake, and a reduced tree growth and forest productivity (Quero et al., 2006; Valladares and Sánchez-Gómez, 2006). Therefore, it would be expected that species adapted to drought have a slow inherent growth rate (but see Fernández and Reynolds, 2000).

The reasons why some species survive drought while others do not, is still not completely understood (Chaves et al., 2002;

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McDowell et al., 2008). Several root- stem- and leaf traits seem to be responsible for the different levels of tolerance to drought stress. For example, the ability to produce more roots than shoots has been positively related to seedling drought survival (Lloret et al., 1999) as it may enhance plant water uptake. Similarly, seedlings with a high root:shoot ratio (R:S) and a low leaf area performed better under drought (Leiva and Fernández-Aléz, 1998). However, in a field experiment with eight Mediterranean woody species, Matías et al. (2012) did not find a clear trait related to drought response.

Not only biomass allocation to roots, but also rooting depth is important, as water availability is higher in deeper soil layers. Woody species from drier environments with a longer dry season have deeper roots (Filella and Peñuelas, 2003; Sack et al., 2003; Markesteijn and Poorter, 2009), and higher maximum rooting depth per leaf area (Paz, 2003). Other root morphological traits can be related to drought tolerance. Root morphology can be described with the specific root length (SRL), which indicates how much root length can be build per unit of root mass (Ryser, 2006). A high SRL can be an advantage in water-limited conditions (but see Wright and Westoby, 1999), as maximizing SRL means an increased root–soil interface for the same carbon investment, and hence, a higher root absorption potential (Eissenstat, 1992).

Continued water transport during drought depends also on stem traits, such as wood density (WD). Tropical tree species with high WD are more cavitation resistant than species with low WD (Markesteijn et al., 2011), probably because they have narrower vessels and structurally better enforced stem material, that is more resistant to vessel implosion. In contrast, species with low WD have fast growth because of their low stem construction costs, and because the high assimilation rates that come along with their conductive stem tissues (Ter Steege and Hammond, 2001; Santiago et al., 2004).

Leaf traits determine water loss, and are therefore closely related to drought tolerance (Tardieu, 2005). A high specific leaf area (SLA) implies a high surface to volume ratio of leaves, and hence high water loss. Similarly, high photosynthetic rates imply high transpiration rates, and hence, lower drought tolerance (Valladares and Sánchez-Gómez, 2006).

This study focuses on Mediterranean ecosystems, because they are especially strongly limited by a long and intense drought period that coincides with the hottest period (with maximum daily temperatures up to 45 °C). Moreover, in the next decades, the Mediterranean region of the Iberian Peninsula is predicted to face a 20% decrease in precipitation, and an increase of 2–3 °C in temperature (MARM, 2009), all of which will lead to higher water stress. Plant establishment in the Mediterranean region is currently severely limited by drought (Rey and Alcántara, 2000; Quero et al., 2008; González-Rodríguez et al., 2011) and climatic predictions and field simulations suggest that this will become even more problematic in the future (Matías et al., 2012).

Here, a dry-down experiment was carried out with seedlings of 10 Mediterranean woody species where 17 key morphological and physiological traits were measured, with the main objective to test whether they are indeed important for the drought survival and distribution of species. This study focused on seedlings, as they are especially vulnerable to drought because of their limited root systems (Tyree et al., 2003; Markesteijn and Poorter, 2009). The experiment was carried out under controlled conditions, to be able to compare species under the same stress conditions, which is difficult to realize in the field. Most experimental drought studies compare plant performance under low and high water availability (e.g. Sack, 2004). The strength of this study resides in the fact that a dry-down experiment was done, thus simulating plant performance when the plants enter the dry season, which presents the major bottleneck for their survival. Another strong point is that many plant traits were included, as growth and its components (LAR and NAR), biomass allocation, and morphological and physiological leaf and root traits which allow to tease apart which traits are the strongest drivers of drought performance.

The following hypotheses were tested: (i) seedlings of 10 Mediterranean woody species differ strongly in their response to drought, (ii) specific functional traits will be good predictors of survival under drought, and different plant strategies can be distinguished based on functional traits and drought response, and (iii) drought survival and its underlying traits can explain the observed species distribution patterns in the field.

2. Material and methods

Research was carried out in a greenhouse at the University of Córdoba (37° 51′ N, 4° 48′ W; at an altitude of 100 m; Spain), between May 2009 and July 2010. During this period, temperature in the greenhouse was 18.8 ± 4.6 °C (mean of 14 months ± SD, with a maximum of 41 °C in summer period -on average-), relative humidity was 29.7 ± 21% and irradiance on a clear day (measured at 13.30 PM solar time, 29th of July of 2009) was 428 ± 128 μmol m^{-2} s^{-1}.

Ten Mediterranean woody species were selected from different families, differing in leaf habit (deciduous and evergreen), growth form (shrub and trees) and distribution along a drought gradient in the field (Table 1), thus adding ecological reality, and allowing for a stronger generalization of the results. To describe the position of species along the drought gradient, a mean Drought Distribution Index (DDI) was assigned to each species, based on the expert judgement of 5 researchers (see Table S2 Supplementary data on line for researchers information), following the criteria of Niinemets and Valladares (2006), which served to establish the different ranges. DDI varied from 1 (very intolerant); 2 (intolerant); 3 (moderately tolerant); 4 (tolerant) and 5 (very tolerant), based on the characteristics of the habitat distribution of the species (see Table 1 for species ranking).

2.1. Experimental design

The experiment consisted of two phases: a six-months growing phase (from May to October 2009), in which plants were grown under favourable growth conditions and watered three times a week to field capacity; and a nine-month dry-down phase (from October 2009 to July 2010) in which watering was withheld, and seedlings were exposed to acute drought until they died. At the same time a control group (5 seedlings per species) was periodically watered, which served as a comparison for the drought treatment.

2.2. Growing phase

One-year old seedlings were obtained from the San Jeronimo nursery (Consejería de Medio Ambiente, Junta de Andalucía, Spain). Seedlings were transplanted to 4.33 L PVC pots of 50 cm height and 10.5 cm diameter. Such deep pots allow deep root development without much root distortion. The substrate was a mixture of sand, peat and vermiculite (4.5:2:1). To avoid nutrient limitation, 10 g of slow release fertilizer (Plantacote Plus, NPK 14:9:15, Aglukon, Valencia) was added to each pot, and all pots were watered three times a week to field capacity. The first two months (May and June, 2009), pots were randomly distributed in a nursery (62 individuals per species; 620 plants in total). Once all plants had acclimated, a first harvest was carried out for 12 individuals per species (see methods below). Then, pots were moved to the greenhouse (now there were 50 individuals per species, 500 plants in total). Most