



Ecological implications of different water use strategies in three coexisting mediterranean tree species



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ABSTRACT

The ability of trees to grow and survive during periods of water scarcity is determined by the water use strategy of each individual. In this study we evaluated how water use strategies can influence the establishment phase of three coexisting species in forests where harvesting intensity and silvicultural interventions have been reduced over recent decades. We conducted a greenhouse experiment between February and July, applying two watering regimes (moist and dry) to current year seedlings in 1.5 m high pots to avoid root growth constraint. At the same time, the physiological performance of seedlings of the same species was monitored under natural conditions in the field over a period of decreasing soil moisture. Our results indicated that resprouter species allocated more than 40% of total biomass to roots whereas the non-resprouter *P. pinea* allocated only 26%. The plasticity index for the root traits was highest in *Q. ilex*, in which the highest stomatal conductance was measured in early summer. The slowest growth and lowest root plasticity, root hydraulic conductance and leaf water potential were measured in *J. oxycedrus*. The three species exhibited a positive carbon balance under low water availability. Coexisting species displayed a continuum in the water use strategies adopted. *P. pinea* would be the least competitive species under the forecasted increasing drought conditions in contrast to *J. oxycedrus*, which presents traits more suited to coping with droughts.

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1. Introduction

The speed of anthropogenic climate change can exceed the ecological amplitude for adaptation in many species. Hence, the current regeneration niches of many species are expected to change (Williamson et al., 2009). However, the forecasted poleward migration of the species (Woodall et al., 2009; Ruiz-Labourdette et al., 2010) may be an over-simplification of what is a more complex phenomenon of interactions between temperature and precipitation that affect species differently (van der Wal et al., 2013). In this regard, either the capacity for adaptation to environmental stresses (plasticity) or the ability of a single species to compete for limited resources in a mixed forest can determine variations in species composition and distribution. Increased competition for the water resources under a climatic change scenario may jeopardize growth and survival, especially in younger plants (Matzner et al., 2003).

The ecophysiological and morphological traits specific to each species are strongly related to *where* species can regenerate, *which*

species can coexist, and *how* they respond to environmental conditions (Mitchell et al., 2008; Duan et al., 2015). In this regard, understanding the ecophysiological and morphological response of different species to changes in water availability can be essential to predict changes in species distribution, community composition, and forest productivity under global change conditions.

Different studies have found alterations in the partitioning of biomass between above- and below-ground plant components under low water availability (Hernández et al., 2010; Waghorn et al., 2015). This is because plants assume a trade-off in the ability to compete for the above- and below-ground resources, investing more biomass to structures involved in the acquisition of the most limited resources (Aerts et al., 1991). However, although the effect of severe droughts seems to increase root biomass over shoot biomass (e.g. Olmo et al., 2014), this effect is not so clear under moderate drought conditions (Pardos et al., 2006), often resulting in contradictory results among different studies (Meier and Leuschner, 2008; Achten et al., 2010). In addition to water availability, biomass partitioning is also determined by the different regeneration strategies. Resprouting species need to allocate more resources to below-ground organs and consequently tend to show

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a lower shoot:root ratio than coexisting non-resprouting species (Paula and Pausas, 2011). Additionally, the resprouting capacity (Keeley, 2009) is determined by different species-specific responses to tissue loss through fire, herbivory, drought and/or insect attack (Zeppel et al., 2015).

In addition to root allocation, low water availability can also modify morphological traits such as root surface area, root volume, root tissue density or specific root length. The latter allows the economic aspects of root systems to be characterized (Ostonen et al., 2007). Maximisation of the specific root length increases the root-soil interface and thus the root absorption capacity (Larcher, 2003). Moreover, low water availability can affect both the root diametric distribution pattern (Hernández et al., 2010) and the average root diameter, which tends to decrease with low water availability. Several studies have suggested that fine roots reflect responses of plants to stress conditions that may not be perceptible in aerial parts (Vogt et al., 1993), exhibiting shorter lifespan (McCormack and Guo, 2014) and more rapid and intense responses to stress than roots from other diametrical classes (Ostonen et al., 2007; Brunner et al., 2015). On the other hand, the absorption capability of roots not only depends on the soil-root interface but also on the resistance of the root system to water flow defined by the hydraulic conductance of roots (Doussan et al., 1998). Some species form new roots sooner than others and those that form roots more quickly usually have higher hydraulic conductance (Carlson and Miller, 1990).

Root traits are strongly correlated with the physiological traits responsible for the water status of the plant (Hernández et al., 2010). For instance, stomatal conductance tends to increase with whole root hydraulic conductance (Perrone et al., 2012), which in turn is dependent on the average root diameter. Moreover, those plants with higher water use efficiency (higher ratio between net photosynthetic rate and stomatal conductance) tend to show decreased growth (Wang et al., 2012; Olano et al., 2014). In addition to water availability in the soil, plant water status is controlled by environmental factors (such as vapour pressure deficit) and the xylem hydraulic properties of the plant. Higher hydraulic conductance results in enhanced xylem efficiency, which is achieved at the cost of increasing the risk of xylem embolism (Gleason et al., 2016). Species that close stomata early in response to desiccation were found to experience low risk of major xylem cavitation (Skelton et al., 2015). Stomatal closure is the most efficient response against cavitation (Froux et al., 2005), however, it also decreases the net photosynthetic rate and growth. Species that rapidly reduce stomatal conductance while maintaining high water potential are considered to display an isohydric strategy. Anisohydric species show less strict stomatal regulation, extending gas exchange further into the drought period (Skelton et al., 2015) and also displaying lower values of xylem water potential. The latter species tend to be more resistant to cavitation and have denser wood (Meinzer et al., 2008). Therefore, the balance between stomatal regulation and xylem hydraulic properties plays an important role in defining the water regulation niches and ecological strategies of species (Bogeat-Triboulot et al., 2002).

In addition to stomatal regulation, living stem cells can serve as water storage compartments to alleviate imbalances between water loss and uptake (Meinzer et al., 2008), working like a buffering system for smoothing abrupt changes in xylem water potential. Internal water reserves of stems are depleted during the day and subsequently replenished overnight, causing morning shrinkage and evening swelling of the stem diameter (Steppe et al., 2012). Linear variable displacement transducer sensors (LVDTs) provide a useful tool not only to measure stem growth but also to measure daily stem shrinkage in relation to changing levels of hydration. This variable tends to be higher in stressed plants (see for instance Parladé et al., 2001; Daudet et al., 2005; Šimpraga et al., 2011).

Since it is unclear to what extent co-occurring species separate out into the isohydric-anisohydric dichotomy (Skelton et al., 2015), it can be expected that species co-occurring in a mixed forest will show different trade-offs between growth and survival (Cuny et al., 2012) according to their reproductive strategies and adaptive mechanism to cope with stress conditions. With this premise in mind, we carried out a comparative experiment with three Mediterranean species (*Juniperus oxycedrus*, *Pinus pinea* and *Quercus ilex*) coexisting in mixed forests whose management has historically focused on nut production in over-mature productive *Pinus pinea* trees, with firewood extraction from *Quercus ilex* or forage as secondary uses. As these practices have been gradually abandoned, the dynamics of these mixed stands remains unclear.

Our aim was to investigate how the different traits of these three species (two conifers and one broadleaf evergreen species), which exhibit different reproductive strategies (seeder vs resprouting species), leaf type (broadleaf or needles) and growth rate (medium-slow-very slow growing species) combine to create a comprehensive water use/ecological strategy during the early establishment phase, and how this translates into differential responses to climate patterns and potential for successful establishment in a changing environment. More specifically, we hypothesized that (1) in the mixed forests studied there is a continuum in the water use strategies of the species that allows complementarity in the water-use strategies and hydrological niches. Such complementarity may facilitate the co-existence of the three species in a water limited environment; (2) resprouter species (such as *Q. ilex* and *J. oxycedrus*) will present a better suit of traits for coping with severe drought conditions than obligate seeder species (such as *P. pinea*); (3) non-resprouter species will allocate less biomass to roots and grow faster than resprouter species during the establishment phase; (4) species with more plastic root systems will be able to maintain higher stomatal conductance as soil dries out during late Spring and early Summer.

2. Material and methods

2.1. Study site

The stands under study have traditionally been managed for the production of pine nuts. Silvicultural management was oriented towards achieving regular stands dominated by mature over productive *P. pinea* trees. In recent decades the forest uses have changed, and the decrease in silvicultural interventions, together with increased grazing and recurrent forest fires have led to a greater presence of *Q. ilex* and *J. oxycedrus*. *Q. ilex* is often present as a shrub, occupying large areas in the form of a chaparral-type understory rather than as a tree, while *J. oxycedrus* is a less abundant codominant species.

Due to the difficulty involved in studying biomass allocation and root traits in the field (i.e. root extraction and installation of LVDT sensors in the stems of young trees) we carried out a greenhouse experiment to monitor root traits, while the bulk of the physiological performance monitoring was carried out under natural conditions in the field.

2.2. Plant culture and watering

Seeds from the three species under study were collected as a pool sample from different regions of provenance. The *Juniperus oxycedrus* L. (prickly juniper) came from 'Serranía de Cuenca' (40° 14'10.7"N, 1°51'31.8"W) while the *Pinus pinea* L. (stone pine) and *Quercus ilex* L. (holm oak) came from 'Cuenca de Madrid' (40°38'16.4"N, 3°53'56.2"W). Twenty seedlings of each species were transplanted at the end of February to PVC pots of 1.5 m height and

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