



Root hydraulic conductance, gas exchange and leaf water potential in seedlings of *Pistacia lentiscus* L. and *Quercus suber* L. grown under different fertilization and light regimes

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ABSTRACT

Differences in morphology, biomass allocations and physiological responses were investigated in seedlings of Mastic tree (*Pistacia lentiscus* L.) and Cork oak (*Quercus suber* L.) submitted to contrasting fertilization and light regimes during early growth. These species are two evergreen sclerophyllous Mediterranean species frequently used in Mediterranean reforestation programmes. Fertilization was the treatment that affected most of the morphological and physiological variables evaluated in *P. lentiscus* and *Q. suber* seedlings. Leaf area and specific leaf area (SLA) were affected by shading treatment in both species, showing higher values in seedlings grown under shade. *P. lentiscus* seedlings showed a high capacity to modify root morphological variables and root hydraulic conductance (K_R) with the fertilization treatment. In contrast, *Q. suber* showed low to moderate root system changes with the treatments applied, although the fertilization level affected biomass allocation (i.e., root to shoot ratio) in both species. Under high water demand, *P. lentiscus* seedlings with high K_R allowed transpiration (E) to increase without increasing the water potential gradient between soil and leaves. In *Q. suber*, high fertilization induced significant increases in photosynthesis (A), as well as a tendency to increase E with significantly lower leaf water potential (ψ_L).

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1. Introduction

Water stress is one of the main environmental limitations for plants in Mediterranean climate areas (Di Castri, 1981). A long dry season with negligible rainfall, high radiation and high evaporative demand imposes severe stress on plants. These abiotic conditions lead to water deficits that affect many physiological processes and can have consequences for survival and plant growth (Larcher, 2001; Lo Gullo et al., 2003). Species tend to adapt to environmental conditions by different morphological and physiological adjustments (Larcher, 2001; Wood, 2005). This fact is especially important at the seedling stage since seedling establishment and growth in field conditions strongly depend on soil water availability (Vallejo et al., 2000). The capacity of the different species to avoid damaging effects determines their chances of survival and growth (Filella et al., 1998; Vilagrosa et al., 2003).

One of the main morpho-functional traits of species is to optimize water absorption and transport to leaves, thus maximizing their hydraulic system, and this is important when interpreting

leaf physiological behaviour (Tyree et al., 1991; Maherali et al., 1997; Cochard et al., 2002; Bacelar et al., 2007). Water flow through leaves has significant implications for whole plant hydraulics, plant growth, leaf structure, function and ecology. Therefore, limiting the water loss by leaves to a minimum in order to avoid the interruption of water flow in the xylem under conditions of severe drought is of utmost importance (Burghardt and Riederer, 2003). When the threshold is exceeded xylem cavitation occurs and both the growth and survival of the species become compromised (Sperry, 2000; Cochard, 2006). Stomata response has been found to be related to changes in plant hydraulic conductance to prevent desiccation by maintaining the xylem water potential above the minimum threshold (Cochard et al., 2000; Sperry et al., 2002; Vilagrosa et al., 2003). Because the hydraulic conductance determines how much xylem water potential falls below the soil water potential during transpiration, it indicates that there should be a link between the plant's hydraulic traits and the transpirational demand of its foliage (Sperry et al., 1998; Brodrribb and Field, 2000). Moreover, reductions in stomatal aperture to avoid excessive water losses can increase water use efficiency at leaf level, playing an important role in plant response to drought (Cochard et al., 2004; Agele et al., 2005).

In addition to water availability, light and nutrients are two of the most important resources for plant life, and they often interact

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in natural environments (Hirose and Bazzaz, 1998; Lone and Khan, 2007). Soil nutrient availability and light conditions influence the morpho-functional and biomass allocation patterns of development in plants. Previous studies have reported changes in plant morphology and physiological traits as a consequence of different nutrient and light conditions (Villar-Salvador et al., 2004; Barigah et al., 2006; Trubat et al., 2006). Seedlings grown with high fertilization doses have shown high survival and growth under field conditions (Villar-Salvador et al., 2004; Oliet et al., 2009), but these results have been different in environments with strong water limitations (Trubat et al., 2008). Indeed, it has been hypothesized that high-fertilized trees may be more vulnerable to drought stress than low-fertilized ones because of the former's increased aerial size and transpiration rates and decreased allocation to roots (Harvey and Van den Driessche, 1999).

The light environment may also profoundly affect the morphological and physiological characteristics of plants, as it is mainly related to biomass allocation patterns and root system development (Valladares and Pearcy, 1998; Clearwater and Meinzer, 2001). Shading by means of nursery techniques or by means of treeshelters under field conditions has been reported to improve the survival and field establishment of Mediterranean species (Valladares et al., 2000; Sack and Grubb, 2003; Pons and Pausas, 2006; Pérez-Devesa et al., 2008).

The objective of the present study was to analyze the combined effects of nutrient availability and incoming radiation during early growth in two co-occurring Mediterranean sclerophyllous species on the basis of several morphological and physiological traits. Mastic tree (*Pistacia lentiscus* L.) and Cork oak (*Quercus suber* L.) were selected because these species are both common in Mediterranean flora and widely used in reforestation programmes to recover degraded ecosystems. Fertilization and light regimes are known to be important management options in nursery production as their ability to change plant morphological and physiological characteristics can affect seedling performance and drought resistance. We hypothesized that seedlings growing under more stressful conditions (lower nutrients and high light availability) would have a higher capacity to supply water to leaves since they would allocate more resources to belowground than to aboveground parts and, consequently, these seedlings should be able to maintain a better performance.

2. Materials and methods

2.1. Growth conditions

P. lentiscus and *Q. suber* seeds from local provenance were sown in a public nursery (Santa Faz, Alicante, Spain; 38°23'N; 0°26'W; 80 m a.s.l.) in January 2005. The mean annual rainfall is 353 mm and the mean annual temperature is 18 °C. Seedlings were grown for 6 months in 300 cm³ commercial containers (ForestPot®) in a mixture of peat and cocopeat fibre (1:1, v/v). We used a complete factorial design with two factors (nutrient availability and light conditions), each having two levels. The irradiance regimes were full sunlight (FS) and 60% full sunlight (S), as excessive shade is not recommended for Mediterranean plants. Incoming light was manipulated by protecting half of the seedlings with a shade mesh. The photosynthetically active radiation was measured with a Sunfelck Ceptometer (Decagon Devices Inc., Pulman, WA, USA) to determine the incoming radiation received by the seedlings. Around 80 fertilized seedlings per species and treatment were arranged randomly under the different light levels. Nutrient availability was established by applying a slow-release fertilizer (Osmocote®; N:P:K 14:8:14) mixed with the substrate at 2 g l⁻¹ (low fertilization, LF) or 5 g l⁻¹ (high fertilization, HF)

doses. The watering regime was gauged to the seedling water demand.

2.2. Morphological traits

After 6 months, 7 seedlings from each treatment and species were randomly selected for morphological variables determination. Stem height and root collar diameter were measured. Leaves were scanned and leaf area was measured using image analysis software (WinRhizo, Régent Instruments Inc., Quebec, Canada). Specific leaf area (SLA) was calculated as leaf blade area/dry blade mass. Root surface area and root length were measured after washing out the roots, scanning them (on a professional scanner with transparency adapter) and analyzing the images with the same specific analysis software used for the leaves. Biomass fractions of leaves, stems and roots were determined after drying in a forced-air oven at 65 °C to constant weight. Biomass allocation at the plant level was determined between roots and aboveground plant parts, commonly expressed as the root to shoot ratio on a dry weight basis (Cairns et al., 1997).

2.3. Root hydraulic conductance

Whole root system hydraulic conductance (K_R) was measured in 7 plants per treatment in the laboratory. Seedlings were watered to field capacity the night before the measurements. K_R measurements were carried out early in the morning. Root systems were kept in their substrate and perfused with distilled and de-gassed ultra-pure water filtered through a 0.1 μm water filtration membrane using the high pressure flow meter method (HPFM, Dynamax, USA) connected to the stump. K_R was measured in a transient way within a range of 0–0.5 MPa pressures at a constant rate of 3–5 kPa s⁻¹ and the flow rate (F) was recorded every 3 s as described in Tyree et al. (1995). F was plotted versus pressure (P), and K_R was estimated as the slope of a linear regression between both variables ($\Delta F, \Delta P$). K_R was corrected for air temperature. Laboratory air temperature was registered in each measurement and varied no more than 1.5 °C during any set of measurements. Substrate temperature was assumed to be the same as air temperature. We estimated root hydraulic conductance on a leaf area basis (K_{RL}), root hydraulic conductance scaled by total root surface area (K_{RR}), and root hydraulic conductance scaled by root length (K_{RRL}) (Nardini et al., 2000).

2.4. Gas exchange and leaf water potential

Gas exchange measurements were taken in 5 well-irrigated seedlings per treatment and species (a total of 20 seedlings per species) in a climatic chamber Fytotron (Sanyo, Gallenkamp PLC, Leicester). Environmental conditions in the climatic chamber were adjusted so as to submit seedlings to highly stressful conditions. Maximum summer air temperatures of 35–40 °C frequently occur in the Mediterranean maquis (Larcher, 2000). Seedlings were subjected to a photoperiod of 12 h in the climatic chamber (temperature: 35 °C day/25 °C night; relative humidity: 44% day/55% night), with an ambient vapour pressure deficit of 3.15 ± 0.10 kPa during day conditions and a photosynthetic active radiation of 1000 μmol/m² s. Net photosynthesis (A) and transpiration rate (E) were measured at the beginning of the daytime climatic conditions and consecutively in all plants until constant values (about 3 h later). Gas exchange measurements were made at 380 ppm of CO₂ concentration and 1000 μmol/m² s of photosynthetic active radiation by using a portable infrared gas analyzer Li-6400 (Li-COR Biosciences, UK Ltd.). Instantaneous water use efficiency (WUE) was estimated as the ratio between A and E , μmol CO₂ fixed per mmol H₂O used per unit of leaf area and unit of time (Larcher, 2001). When the gas exchange measurements registered in each

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