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Root morphology and water transport of *Pistacia lentiscus* seedlings under contrasting water supply: A test of the pipe stem theory

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Abstract

Restoration of degraded Mediterranean areas often requires the reintroduction of key-stone woody species but the establishment of seedlings of native species is frequently poor. This is partly due to insufficient knowledge of the ecology of these species at the seedling stage. Fast rooting and efficient water supply under water limiting conditions may be crucial to withstand summer drought and ensure establishment. However, knowledge of the relationship between root morphology and the water transport capacity of Mediterranean woody species in response to drought is still scarce. We evaluated the effect of low water availability on biomass allocation, root morphology and transpiration of a common Mediterranean shrub species, Pistacia lentiscus L. Seedlings of this species were grown in pots filled with soil under glasshouse conditions for 6 months, and irrigated either weekly (W+) or monthly (W-). Low water availability strongly reduced all fractions of biomass, and decreased relative biomass allocation belowground. Average diameter of fine roots colonising the soil was higher in W+ plants, but this resulted in only marginal effects on specific root length. Water limitation did not affect the topology of secondary roots colonising the soil. Surprisingly, the ratio of leaf area to coloniser roots surface area was higher in W- seedlings. Sapwood area was strongly correlated with leaf area, secondary roots cross-sectional area, and surface area of fine roots colonising the soil when all seedlings were pooled. In agreement with the pipe stem theory, the ratio of sapwood area to leaf area was not affected by watering regime. Plant water loss when soils were taken to field capacity was significantly correlated with leaf area, sapwood area, secondary roots cross-section area and coloniser roots surface area. Water loss at high water availability was greatly reduced in W- plants, as leaf area decreased and transpiration rates on a leaf area basis were similar in W+ and W- seedlings. P. lentiscus showed limited capacity to acclimate to low water availability by modifying biomass allocation and root morphology. Thus, parallel to what has been observed aboveground, this species can benefit from periods of high water availability by showing relatively high root growth rates, but may respond poorly to water scarcity.

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1. Introduction

In semiarid areas, long-term land use has frequently resulted in the disappearance of woody sprouters (Grove and Rackham, 2001). These species are important for ecosystem functioning because they protect the soil from erosion, recover quickly after disturbance, and promote biodiversity by facilitating other vascular plants, thus providing shelter and food for fauna (Herrera, 1982; Maestre and Cortina, 2005). In degraded semiarid areas, a decrease in anthropic pressure may not be enough to ensure spontaneous colonisation, and species reintroduction may be an essential step in the restoration of these habitats (Whisenant, 1999; Vallejo et al., 2005).

Seedling survival in Mediterranean semiarid lands is usually low, and short-term aboveground growth of seedlings is often negligible due to drought during the first summer after transplanting into the field (Vilagrosa et al., 1997; Maestre et al., 2003; Cortina et al., 2004). The rapid development of a deep root system that can access water stored lower in the soil profile may be essential for successful seedling establishment (Joffre et al., 2002; Otieno et al., 2006). Drought may not only increase the proportion of biomass allocated belowground (Nicotra et al., 2002), but also the geometry of the root system (Fitter, 1986; Taub and Goldberg, 1996; Ryser, 2006). Species native to lower rainfall environments tend to produce roots with

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longer links (Nicotra et al., 2002), and higher specific root length (Poot and Lambers, 2003; Tjolker et al., 2005). Drought may increase the length of root links within a species (Jupp and Newmann, 1987; Fitter and Stickland, 1992; Berntson, 1994). Many plants respond to water limitation by inhibiting lateral branching (Malamy, 2005), and thus forming more herringbonelike root systems (Fitter, 1986; Berntson, 1994). Herringbone systems are considered more efficient in capturing high mobility resources such as water (Fitter, 1991). However, there are exceptions to this general pattern. For example, Taub and Goldberg (1996) found that dicots but not grasses showed this type of response. Furthermore, there was no relationship between rainfall level and root branching pattern in a range of Australian perennial plants (Nicotra et al., 2002). These studies suggest that both species and functional group play a part in determining root responses to water availability.

One way to understand these complex relationships is to study how changes in root system morphology affect plant water transport capacity using the pipe stem theory. This has been used to compare the diameter of stems and roots of different developmental order (Bouma et al., 2001; Oppelt et al., 2001), and to relate the cross-sectional area of conductive tissues to the surface area of transpiring tissues (Shinozaki et al., 1964a,b). For adult individuals of woody species, the ratio of sapwood area to leaf area may increase as water availability is reduced (Callaway et al., 1994; Mencuccini and Grace, 1995; Jackson et al., 1999; Mencuccini and Bonosi, 2001).

Pistacia lentiscus L. (mastic tree) is one of the most important woody species in the Mediterranean Basin, where it is a common part of the climax vegetation in semiarid coastal areas (Tomaselli, 1981). *P. lentiscus* has been proposed as a suitable species for the restoration of semiarid areas due to its adaptations to drought and resistance to disturbance (Vallejo et al., 2000). It also has high root growth capacity (Fonseca, 1999; Trubat et al., 2004) and plasticity to contrasted nutrient availability (Trubat et al., 2006), and responds readily to low water availability by modifying aboveground morpho-functional traits (Vilagrosa et al., 2003). However, little information is available on belowground morpho-functional strategies of this species to withstand drought.

We studied the belowground responses of *P. lentiscus* to contrasting water regimes to test the hypothesis that low water availability would promote biomass allocation belowground, increase the ratio of sapwood area to leaf area, and modify root morphology, thus improving its capacity to supply water aboveground.

2. Material and methods

In spring 2000, *P. lentiscus* seeds collected in the Region of Valencia, Spain were planted into 150 cm^3 plugs filled with a mixture of limed sphagnum peat and cocoapeat (1:1, v:v). In January 2001 in the UK, seedlings were planted into 8 L pots filled with a 3:1 (v:v) mixture of quartz sand and soil. As a surrogate for Mediterranean soil we used a flinty silty clay loam topsoil (Panhole series) of pH 7.9 (0.01 M CaCl₂) collected from the plough layer (23 cm) of an arable field over-

lying chalk on the Rothamsted Estate, Hertfordshire, UK. Total nitrogen was 0.061%, loss on ignition 9.1%, available phosphorus 36.4 mg L^{-1} and exchangeable potassium 214 mg L^{-1} (modified Morgan method).

Pots were watered to saturation in mid January 2001 and kept in a glasshouse throughout the period of study. Average temperature was 24 °C. Plants were either watered weekly (W+ seedlings) or monthly (W- seedlings) with tap water. By July 12 (175 days after the onset of the experiment) W- seedlings had received 4.1 L of water, and W+ seedlings had received 9.0 L of water. Each treatment was replicated 16 times.

On July 13 we estimated transpiration rate from the weight loss of 10 seedlings per treatment (9:00-17:00 GMT; average PPFD 460 μ mol m⁻² s⁻¹; average air temperature range: 25-31 °C). Containers had been previously sealed to avoid evaporation losses. In mid July 2001 we harvested the 16 month-old seedlings and carefully washed out the root system. We separated three root fractions: the first order tap root, higher order roots remaining within the original root plug and higher order roots colonising the pot (hereafter colonisers), and measured the diameter of secondary roots at their proximal end. The cortex was separated at the root collar level, and under the assumption that all xylem was sapwood, we measured the sapwood area. Cross-sectional area of the main secondary roots was also measured. Total root length, total surface area and average root diameter were obtained by using WinRhizo software (Régent Instruments, Québec, Canada) to analyse scanned root images (A3 Epson 836XL flatbed scanner with a transparency adapter operating at 300 dpi. Images were 8-bit greyscale and saved in uncompressed TIFF format).

The topology of root systems can be described by three variables, magnitude, total exterior pathlength and altitude (Fitter, 1985). Magnitude is the number of root tips in the whole root system. Total exterior pathlength is calculated as the sum of all links (internodes) counted from each of the root tips back to the base of the root system. Altitude is the single longest individual path from a root tip back to the base link. We counted the number of root tips and calculated the topological indices of root system altitude and root system total external pathlength for a randomly chosen secondary colonising root from each pot, according to the method of Werner and Smart (1973) as modified by Berntson (1995).

Leaves were scanned and analysed as for roots to obtain leaf area. All biomass fractions were dried at 65 °C for 3 days to determine the dry weight. We estimated the root weight ratio (RWR) of coloniser roots as the ratio between coloniser roots and that of the whole root system. Both the ratio between total belowground and total biomass (RWR for the whole root system), and the RWR of coloniser roots were analysed by using the natural logarithms of both terms of the ratio. Specific root length (SRL) was estimated as the ratio between root length and biomass.

Treatment effects were evaluated by using one-way ANOVA with one fixed factor (water). For topological analyses, the magnitude of the root system (number of tips) was included in the analysis as a covariate. We used Pearson correlation coefficients to explore the relationship between pairs of variables. Variables Download English Version:

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