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Long term responses and adaptive strategies of *Pistacia lentiscus* under moderate and severe deficit irrigation and salinity: Osmotic and elastic adjustment, growth, ion uptake and photosynthetic activity

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ABSTRACT

Pistacia lentiscus is a wild species that grows widely in the Mediterranean area. However, despite it appearing to be particularly resistant to some stressful conditions, drought and salinity may alter its physiological and morphological behavior. While the responses of *P. lentiscus* to both stresses have been partially studied, its avoidance and tolerant mechanisms are poorly understood. In particular, changes in leaf tissue cell wall and the photosynthetic activity during a prolonged water deficit and salinity are unknown. Nursery grown plants were subjected to four irrigation treatments lasting eleven months: control ($1\ dS\ m^{-1}$, 100% water holding capacity), two deficit treatments (moderate and severe water deficit, corresponding to 60 and 40% of control) and saline treatment ($4\ dS\ m^{-1}$, same amount of water supplied as control). Biomass accumulation was affected more by deficit irrigation than by salinity. Salt tolerance in *P. lentiscus* was associated with the restricted uptake of Cl^- and its storage in roots. However, the cumulative effect of irrigating with saline water involved an over-accumulation of Na^+ and Cl^- in leaves, which probably contributed to the pronounced decrease in photosynthesis, confirming the importance of the length of exposure of the plants to salt stress. Plants under saline or severe deficit irrigation exhibited slight dehydration throughout the experiment, as indicated by the lower leaf water potential and relative water content, due to the low availability of substrate water (osmotic effect). The response of plants to severe water stress, which resulted in stomatal closure and a decrease in net photosynthesis rate, involved a marked decrease in plant height and growth, especially in the first months of the experiment, after which a slight acclimation may have occurred in these plants. Under moderate water stress, most of these responses were mitigated. Salinity induced active osmotic adjustment and decreased leaf tissue elasticity. Due to its tolerance of water stress and salinity, *P. lentiscus* is a suitable ornamental species for gardening in arid and saline area.

1. Introduction

Drought tolerance in plants may be explained by functional and structural adaptations at cellular and whole plant, such as growth regulation, osmotic adjustment, changes in cell wall elasticity and in leaf water potential, stomatal closure, all of which may help alleviate the harmful effects of stress (Zheng et al., 2010; Suárez, 2011). Exposure to salt may affect plant metabolism through an osmotic effect, causing water deficit, or through a specific ion effect, causing excessive ion accumulation (Azza Mazher et al., 2007). Under saline conditions, plants have to activate different physiological and biochemical mechanisms to cope with the salt stress, which include changes in morphology, anatomy, water relations, photosynthesis, the hormonal profile, toxic ion distribution and antioxidative metabolism response (Acosta-Motos et al., 2017). However, although salinity and drought stress are physiologically related and the tolerance mechanisms

Abbreviations: C, control; DW, dry weight; EC, electrical conductivity; g_s, stomatal conductance; J, absorption rate of ions by the root system; LMA, leaf mass per area; P, significance; P_n, net photosynthesis rate; P-V, pressure-volume; RWC_{tpl}, relative water content at turgor loss point; S, saline treatment; SW, severe water deficit treatment; MW, moderate water deficit treatment; Ψ_l, leaf water potential; Ψ_{100s}, leaf osmotic potential at full turgor; Ψ_{tpl}, leaf water potential at turgor loss point; ε, bulk modulus of elasticity; F_v/F_m, maximal PSII photochemical efficiency

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overlap, some aspect of plant physiology and metabolism may differ if the plant experiences saline or water stress. In particular, the changes in leaf tissue cell walls and the factors limiting photosynthesis under these conditions and their possible interactions with leaf tissue damage are not well understood. However, while some Mediterranean species appear to be particularly resistant to some stressful conditions and have developed mechanisms/strategies, such as efficient stomatal control linked to a conservative use of water resources and increases in the water uptake with deep root systems that may allow plants to survive during intense drought conditions, this does not necessarily mean that the plant will be of high visual quality. Even plants that have some degree of drought and/or salinity tolerance may show reductions in quality when exposed to these stresses, which is an important factor in ornamental plants destined for use in gardens and landscaping (Cameron et al., 1999).

The use of Mediterranean shrubs for revegetation in semiarid areas has increased in recent years due to its ability to adapt to severe conditions of drought, which is considered one of the most important factors affecting plant survival and species distribution (Filella et al., 1998; Vallejo et al., 2000; Vilagrosa et al., 2014). Among these, *Pistacia lentiscus* L. (mastic tree or lentisc), is considered a good alternative for landscaping and restoration projects because it responds well to the conditions of Mediterranean summers. The effect of severe drought on the physiological and morphological parameters of *P. lentiscus* and its strategies of drought-avoidance have been well established by Vilagrosa et al. (2003a, 2010) and by Gratani et al. (2013). Indeed, many studies in plants in water-limited ecosystems have regarded the role of plant hydraulic conductivity and their relationship with other traits as a key step in plant growth and survival (Vilagrosa et al., 2010; Lens et al., 2013). Although the general effects of withholding irrigation during the summer period on plant growth and survival of *P. lentiscus* have been studied (Vilagrosa et al., 2003a), further work is required to quantify its physiological responses to different levels of deficit irrigation, as in urban gardening projects, unlike in most revegetation projects, plants are usually watered and fertilized as needed, or at least partially watered to maintain an acceptable appearance. Such deficit irrigation strategies involve the application of water at a volume lower than that needed to compensate the evapotranspiration rate, and may be used in potted ornamental plants to improve plant quality by reducing excessive vigour and promoting a more compact habit (Cameron et al., 2006). However, the degree and duration of the water stress imposed on each species is also critical (Álvarez et al., 2009). In this sense, numerous works in ornamental plants have demonstrated that plant quality decreases as the severity of deficit irrigation increases (Hansen and Petersen, 2004; Henson et al., 2006; Katsoulas et al., 2006; Chyliński et al., 2007; Silber et al., 2007; De Lucia, 2009; Álvarez et al., 2009; Sánchez-Blanco et al., 2009; Bolla et al., 2010; Andersson, 2011; Bernal et al., 2011).

Furthermore, as the competition for high quality water increases, the use of saline waters and reclaimed water has become an option for irrigating ornamentals plants in urban gardening (Cassaniti et al., 2009; Acosta-Motos et al., 2014; Acosta-Motos et al., 2016). Tattini et al. (2006) and Tattini and Traversi (2008) tested the influence of salinity on *P. lentiscus* during a short period of intense salinity, and found it to be particularly tolerant to salt stress, although growth was markedly reduced, at least using irrigation water of 23 dS m^{-1} (200 mM NaCl). In addition, Armas et al. (2010) conducted a study to determine species' tolerances to salinity and found that *P. lentiscus* can withstood salinity levels similar to that of groundwater, reached 25.3 dS m^{-1} (220 mM NaCl). However, it is well known that plant response to salinity depends not only on the intensity of salt treatment, but also on the time of exposure to the salt treatment (Álvarez and Sánchez-Blanco, 2015). These important aspects must be considered when saline water is used for irrigation in long-lived species, as the interaction of both parameters will determine the physiological and molecular changes that take place. Since the growing season also seems to affect the response of shrubs to salt or water deficit (Valdez-Aguilar et al., 2011; Álvarez et al., 2013), the present research was carried out during the entire growing season using different deficit irrigation levels and water quality.

The purpose of this work was to study the long-term effects on *P. lentiscus* plants in response to saline water and water deficit. For this, growth, ion uptake, gas exchange, leaf water potential and their components, oxidative damage and photosynthesis responses were evaluated to ascertain the changes that take place in plants exposed to different levels of deficit irrigation and salinity. Understanding the limits and trade-offs between drought and salt tolerance, and the traits that are associated with tolerance to both factors, would provide important insights that would contribute to water management in the Mediterranean area, where deficit irrigation strategies using low quality waters are very often applied in gardening and landscaping projects.

2. Materials and methods

2.1. Plant material and experimental conditions

Seedlings of 1-year-old *Pistacia lentiscus* (mastic) grown in 5 × 5 × 11 cm pots by a specialised nursery were transplanted into 4 L plastic pots (15 × 15 × 20 cm) filled with a 5:4:1 (v/v/v) mixture of coconut fibre, black + sphagnum peat and perlite amended with 2 g L^{-1} of Osmotocote Plus (14:13:13 N, P, K plus microelements). Plants were placed in a plastic greenhouse equipped with a cooling system, located in Santomera, Murcia, Spain (38°06′N, 1°02′W, 110 m a.s.l.). All the plants were watered daily for 4 weeks to field capacity prior to starting the treatments. The micro-climatic conditions, registered with a Hoboware Lite Data Logger (Escort Data Loggers, Inc., Buchanan, Virginia, USA), were 12.9 °C (mean minimum), 25.5 °C (mean maximum) and 20.3 °C (average) temperature; and 42% (mean minimum), 77% (mean maximum) and 62.9% (average) relative humidity.

2.2. Treatments

Pistacia lentiscus plants were subjected to four irrigation treatments (40 plants per treatment) lasting 11 months using a computer-controlled drip irrigation system. The irrigation treatments consisted of a control (C) corresponding to 100% water holding capacity (leaching 15% (v/v) of the applied water), using tap water where the electrical conductivity of the water was 1.0 dS m^{-1}, a saline treatment (S) using tap water with salt added to reach 44 mM NaCl (4.0 dS m^{-1}) and two deficit irrigation treatments: (60% of the control level of irrigation water, 1.0 dS m^{-1} (moderate water deficit; MW) and 40% of the control irrigation water, 1 dS m^{-1} (severe water deficit; SW). One drip nozzle, delivering 2 L h^{-1} per plant, was connected to two spaghetti tubes (one on each side of every pot) and the duration of each irrigation episode was used to vary the amount of water applied, which depended on the treatment and on weather conditions. All the plants were irrigated daily.

2.3. Growth and physiological measurements

At the beginning and at the end of the treatment period ten plants per treatment were separated into shoots (leaves and stem) and roots before being oven-dried al 80 °C until they reached a constant weight to measure the respective dry weights (DW). Leaf area was determined in the same plants, using a leaf area meter (Delta-T Devices Ltd., Cambridge, UK). Leaf succulence was calculated by dividing the fresh by the dry weight and leaf mass per area (LMA) was calculated by dividing the dry weight by the leaf area. Throughout the experiment, plant height was measured periodically in 30 plants per treatment. At the beginning and at the end of the experimental period, ten plants per treatment (separated into leaves, stem and roots) were washed with distilled water and dried at 80 °C, before being stored at room