Application of deficit irrigation in *Phillyrea angustifolia* for landscaping purposes

S. Álvarez[a,b,*], M.J. Gómez-Bellot[a], J.R. Acosta-Motos[c], M.J. Sánchez-Blanco[a]

[a] *Departamento de Riego, Centro de Edafología y Biología del Segura (CEBAS-CSIC), P.O. Box 164, 30100 Murcia, Spain*
[b] *Unidad de Cultivos Leñosos y Hortícolas, Instituto Tecnológico Agrario de Castilla y León (ITACYL), Ctra. Burgos Km. 119, 47071 Valladolid, Spain*
[c] *Universidad Catolica, San Antonio de Murcia, Campus de los Jeronimos, 135, 30107 Guadalupe, Spain*

ABSTRACT

Phillyrea angustifolia is an evergreen shrub of interest for urban landscape design, as well as for use in re-vegetation projects in Mediterranean areas, which are characterized by an acute scarcity of water. The effect of different levels of water deficit on several physiological, ornamental and morphological parameters of *Phillyrea angustifolia* plants was studied to evaluate their adaptability to xerogarden and/or landscape conditions. Nursery grown plants were subjected to three irrigation treatments: a control (watered to container capacity) and two deficit irrigation treatments of 60 and 40% of the amount of water supplied in the control treatment (moderate and severe deficit irrigation). After 23 months, plant height was significantly inhibited by both water deficit treatments, although plant compactness (foliar area in relation to plant height) was not affected. Plants under severe deficit irrigation increased their root to shoot ratio and water use efficiency, which are positive aspects for hardening. Plants exposed to both deficit irrigation treatments exhibited slight dehydration throughout the experiment, especially in spring, as indicated by the lower leaf water potential and relative water content. The tolerance of *P. angustifolia* to drought was mainly related to adjust osmotic and regulated stomatal closure. It is concluded that both deficit irrigation treatments can be used successfully in *P. angustifolia* plant production to reduce water consumption while maintaining good overall quality. Moderate deficit irrigation is specially recommended for gardening purposes, since this treatment produced plants with of visual quality. Severe deficit irrigation is more suitable for landscaping purposes, as an effective nursery technique to produce plants better adapted to environmental stress during transplanting.

1. Introduction

Of all abiotic stresses, drought is the major constraint affecting plant physiological processes, causing huge production losses in agriculture and imposing strong limitations to the establishment and management of green spaces in cityscapes (Toscano et al., 2019). Water scarcity is very common in many areas of the world, and, together with increased industrialization, rapid population growth and climate change, have resulted in important water resource problems, especially in urban environments (Lea-Cox and Ross, 2001; Nazemi Rafi et al., 2019a).

Water conservation in cityscapes is of great importance, as a considerable fraction of municipal water resources in urban areas (nearly 25%) is used for irrigation of municipal landscapes and gardens in urban communities (Zollinger et al., 2006; Welsh et al., 2007; Sun et al., 2012). In this context, managing global water resources is one of the most pressing challenges of the twenty-first century and there is a considerable pressure in agriculture to produce crops more efficiently by reducing water use (Fulcher et al., 2016; Caser et al., 2017). The same applies to irrigated urban landscapes (Cirillo et al., 2013).

Therefore, in order to mitigate water demand conflicts, managers are seekingto achieve significant long and short-term conservation strategies (Brown et al., 2004; Nazemi Rafi et al., 2019a), for example by using precision landscape irrigation (Kjelgren et al., 2000), reclaimed water (Hilaire et al., 2008; Gómez-Bellot et al., 2013), native

and drought tolerant plant species (Lockett et al., 2002), applying deficit irrigation strategies (Mansour et al., 2017; Sánchez-Blanco et al., 2019) and identifying the varying water needs involved in the developmental stages (Stabler and Martin, 2000; Álvarez et al., 2013). Surprisingly, relatively little research has quantified irrigation requirements of ornamental plants, although they constitute a major part of horticultural production and such knowledge would offer great possibilities for water conservation in landscaping (Henson et al., 2006). Moreover, the determination of the minimum watering level for acceptable ornamental quality has not been much investigated (Cameron et al., 2006).

Ornamental native plants, and particularly shrubs are widely used in revegetation and xerogardening projects in Mediterranean regions because of their potential adaptation to adverse environmental conditions, such as drought and salinity, which represent the strongest limiting factors for plant growth and survival (Vilagrosa et al., 2010; Álvarez et al., 2012, 2018; Nazemi Rafi et al., 2019b).

Several ornamental plants, particularly shrub and bush species, have evolved particular combinations of structural and physiological traits to cope with drought, salinity and high solar irradiation stresses (Tattini et al., 2002; 2005; 2006). Therefore, they provide interesting models for study because they not only provide relevant additional information on general stress tolerance mechanisms in plants, but also furnish know-how on their adaptability for use in landscaping and urban greening (Acosta-Motos et al., 2014; 2017; Cassaniti et al., 2009; Cirillo et al., 2014; Kumar et al., 2017; Carillo et al., 2019).

Phillyrea angustifolia L., is a member of the Oleaceae family and an evergreen sclerophylluos largely distributed through dry/warm areas of the Mediterranean Basin (Gucci et al., 1997; Tattini et al., 2006). Most *Phillyrea* show some degree of tolerance to environmental stresses such as drought (Peñuelas et al., 1998; Filella et al., 1998; Mira et al., 2017). They are also known for their high salt tolerance (Tattini and Traversi, 2008; Tattini et al., 2002, 2006; Gugliuzza et al., 2013a). It is for these reasons that *Phillyrea* species is currently being investigated for their potential to restore vegetation in dry-land areas of the Mediterranean Basin, which may suffer from drought during the warm summer season.

In this sense, the effect of severe summer drought conditions, produced by withholding irrigation, on the physiological and morphological parameters of field grown *P. angustifolia* plants and its drought-avoidance strategies have been well established by Peñuelas et al. (2004) and by Vilagrosa et al. (2014). Moreover, the prolonged water stress resulting from low rainfall and high temperatures in summer in the Mediterranean ecosystem may alter the plant's physiological and morphological behaviour, being summer drought considered the most critical factor for the establishment of seedlings after transplanting (Sánchez-Blanco et al., 2014). Thus, transplantation from a nursery to the landscape or xerogarden creates a stressful transition period, which is critical to the establishment, performance and survival of these plants (Franco et al., 2006). In this sense, earlier studies indicated the need to harden plants to reduce the problems associated with drought (Franco et al., 2001, 2011; Bañón et al., 2004; Fernandez et al., 2006).

Numerous studies in ornamental plants have pointed to the importance of factors such as the degree of water stress imposed, and the timing and duration of the same on each species (Navarro et al., 2009; Álvarez et al., 2009, 2013). Thus, a desirable level of deficit irrigation during the hardening phase may result in stocky stress-resistant seedlings, but if the water restriction is too severe the effects may be negative and plants will die. The goal of seedling pre-conditioning is to produce sturdy plants that have a high level of photosynthetic reserves and adequate morphological characteristics, enabling rapid establishment and resumption of growth once in the landscape (Franco et al., 2006). Although the general effects of withholding irrigation during the summer period on the growth and survival of *P. angustifolia* have been studied (Peñuelas et al., 2004), further work is required to quantify its physiological responses to water management in the nursery to optimize the production of high quality plants. For all this, increasing our

understanding of the morphological and physiological shoot and root responses of plants to water management in the nursery is critical for optimising the production of high quality plants.

Gugliuzza et al. (2013b) tested the influence of different water regimes on *P. angustilofia* over a period of 3 months, and found it to be relatively tolerant to water deficit mainly due to decreased growth reduction and a good performance, which could make this drought tolerant ornamental shrub an interesting plant material for the establishment and management of urban green spaces under water-limited conditions, providing different solutions to cityscapes of semi-arid Mediterranean environments.

However, while drought-tolerant species have developed mechanisms, such as efficient stomatal control linked to conservative use of water resources and increased the water uptake through deep root systems, allowing plants to alleviate the harmful effect of water stress and grow during stressful conditions, this does not necessarily mean that the plants require little water for high visual quality (Cameron et al., 1999; Álvarez et al., 2012, 2018; Sánchez-Blanco et al., 2002; Augé et al., 2003). In ornamental plants production destined for use in gardening, quality depends strongly on visual quality (suitable aesthetic appearance and plant fitness) (Nazemi Rafi et al., 2019a; Stabler and Martin, 2000), unlike in revegetation projects, where other features are considered of interest, such as the structure of the root system or biomass partitioning.

The short-term response in terms of growth to deficit irrigation during the warm summer season in *P. angustifolia* have been well described in previous studies (Fernandez et al., 2004, 2006; Gugliuzza et al., 2013b), bit little is known about its physiological and ornamental responses to different levels of deficit irrigation.This is important beause 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. Further work is needed to characterize and quantify the responses in terms of ornamental traits to water shortage. This knowledge is critical for optimizing sustainable high-quality production without compromising the economic value of the crop (Cameron et al., 2006; Franco et al., 2006; Caser et al., 2017)

Moreover, it is well known that plant response to water stress depends not only on the intensity of deficit treatment, but also on the time of exposure to the stress (Álvarez and Sánchez-Blanco, 2013; Álvarez et al., 2018). Hence, carryover effects from year to year need to be assessed when deficit irrigation is used in long-lived species, as the interaction of both parameters will determine the physiological and molecular changes that take place (Mirás-Avalos et al., 2016). Since the growing season also seems to affect the response of shrubs to abiotic stresses (Valdez-Aguilar et al., 2011; Álvarez et al., 2013), the present research was carried out during two growing seasons (24 months), using different deficit irrigation levels in order to evaluate the sustainability of the strategies considered as well as to identify the most appropriate deficit irrigation strategy for each situation, which would contribute to better water management in the Mediterranean area.

Based on these considerations, the aim of this work was to study the long-term effects on *P. angustifolia* plants in response to water deficit, which may occur during the nursery phase or gardening conditions. The drought-tolerance of *Phillyrea angustifolia* was compared in terms of growth, ornamental traits, water relations, gas exchange and partitioning between organs to ascertain the changes that take place in plants exposed to different levels of deficit irrigation during the nursery phase and whether these changes confer stress-resistance to the plant for gardening and/or revegetation purposes.

2. Materials and methods

2.1. Plant material and experimental conditions

Rooted cuttings of 1-year-old *Phillyrea angustifolia* grown in

$5 \times 5 \times 11$ cm pots by a specialised nursery were transplanted into 4 L plastic pots (17 x 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.

2.2. Treatments

Philyrea angustifolia plants were subjected to three irrigation treatments (30 plants per treatment) lasting 23 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) and two deficit irrigation treatments: (60% of the control level of irrigation water (moderate deficit irrigation; MDI) and 40% of the control irrigation water (severe deficit irrigation; SDI). 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 using tap water where the electrical conductivity of the water ranged between 0.8 and $1.0 \, dS \, m^{-1}$.

2.3. Growth and plant water measurements

At the beginning and at the end of the treatment period eight plants per treatment were separated into leaves, 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 weight by the dry weight, and specific leaf area (SLA) was calculated by dividing the leaf area by the leaf dry weight. In addition, the root to shoot ratio was determined in these plants and calculated by dividing root DW by leaf DW. Throughout the experiment, plant height was measured periodically in 25 plants per treatment and the relative growth rate (RGR) was calculated as the rate of increase of height per unit of initial plant height. Compactness was calculated dividing leaf area by the respective plant heights.

Chlorophyll fluorescence, leaf color and relative chlorophyll content (RCC) were periodically measured at midday, on the adaxial leaf surface. The values of maximum photochemical efficiency of photosystem II (F_v/F_m) were obtained using a portable fluorometer Opti-Sciences (Model OS 30; Opti-Sciences Inc., Tyngsboro, MA, USA) on five leaves re-darkened for 20 min before starting the measurements (Camejo et al., 2005). Leaf colour was measured with a Minolta CR-10 colorimeter, which provided the colour coordinates lightness (L*), chroma (C*) and hue angle (h°) (McGuire, 1992), using eight leaves for each treatment and RCC was measured with a Minolta SPAD-502 chlorophyll meter in 20 plants per treatment. The rate of passive ion leakage from stress-sensitive plant tissue can be used as a measure of alterations in membrane permeability. In our case, ion leakage was estimated at the end of the experiment with five replicates per treatment in mature leaves, according to the method described by Lafuente et al. (1991).

The substrate water content was periodically determined using time domain reflectometry (TDR) equipment (Tektronic, model. 1502B) in ten plants per treatment. Throughout the experimental period, changes in leaf water potential (Ψ_l), relative water content (RWC), stomatal conductance (g_s) and net photosynthetic rate (P_n) were determined in seven plants per treatment in mature leaves at midday. Ψ_l was estimated according to the method described by Scholander et al. (1965), using a pressure chamber (Soil Moisture Equipment Co, Santa Barbara, CA, USA), for which leaves were placed in the chamber within 20 s of collection and pressurised at a rate of $0.02 \, MPa \, s^{-1}$ (Turner, 1988),

while the RWC of leaves was calculated according to Barrs (1968). Leaf osmotic potential at full turgor (Ψ_{100s}) was measured in five plants per treatment, using excised leaves with their petioles placed in distilled water overnight to reach full saturation. Leaves from the Ψ_{100s} measurements were then frozen in liquid nitrogen (-196 °C) and stored at -30 °C. after thawing, the osmotic potential was measured in the extracted sap using a Wescor 5520 vapour pressure osmometer (Wescor, Logan, UT, USA), according to Gucci et al (1991). Gas exchange parameters (g_s, P_n) were determined using a gas exchange system (LI-6400, LI-COR Inc., Lincoln, NE, USA), while the P_n/g_s ratio was used as an estimation of the intrinsic water use efficiency. Water use efficiency of production (WUE) was calculated at the end of the experiment by dividing the increment in DW by the water used.

2.4. Statistical analyses of data

In the experiment 30 plants were randomly assigned to each treatment. The data were analyzed by one-way ANOVA using SPSS 17.0 software (SPSS Inc., 2002). Ratio and percentage data were subjected to an arcsine square-root transformation before statistical analysis to ensure homogeneity of variance. Treatment means were separated with Duncan's Multiple Range Test. Statistical comparisons were considered significant at P ≤ 0.05.

3. Results

3.1. Plant water relations, gas exchange parameters and osmotic adjustment

The volumetric water content of the substrate at midday reflected the different irrigation treatments and the climatic conditions. It was highest in the control plants and decreased proportionally with the deficit level imposed with respect to the control (Fig. 1). This pattern was reflected in the seasonal values of the leaf water potential at midday (Ψ_l), which decreased in the water deficit treatments, especially in the SDI plants, in which values of -2.2 MPa were reached in April (Fig. 2A). Leaf water potential at midday (Ψ_l) decreased in all irrigation regimes as the evaporative demand of the atmosphere increased, showing maximum values in winter and minimum values in spring, when environmental conditions became stressful (16–19 months after transplanting). At this time, both deficit irrigation plants had lower Ψ_l values than the control. After this period, the Ψ_l values gradually increased in all treatments, despite the fact that this period coincided with summer (19–23 months after transplanting). At the end of the experiment (September, the end of summer, 23 months after
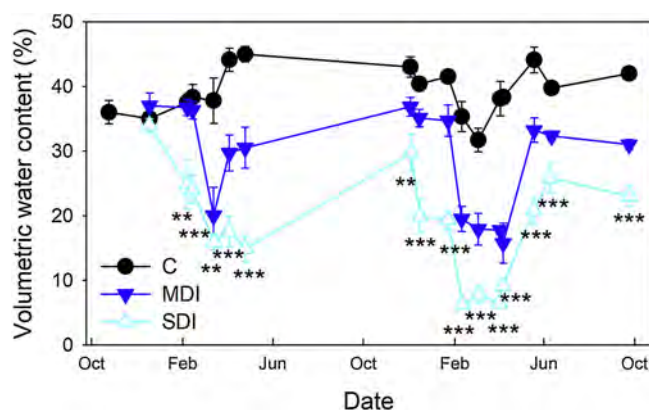

Fig. 1. Evolution of the volumetric substrate water content in *P. angustifolia* plants submitted to different irrigation treatments. Values are means s.e., n = 10. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (**P < 0.01, ***P < 0.001).
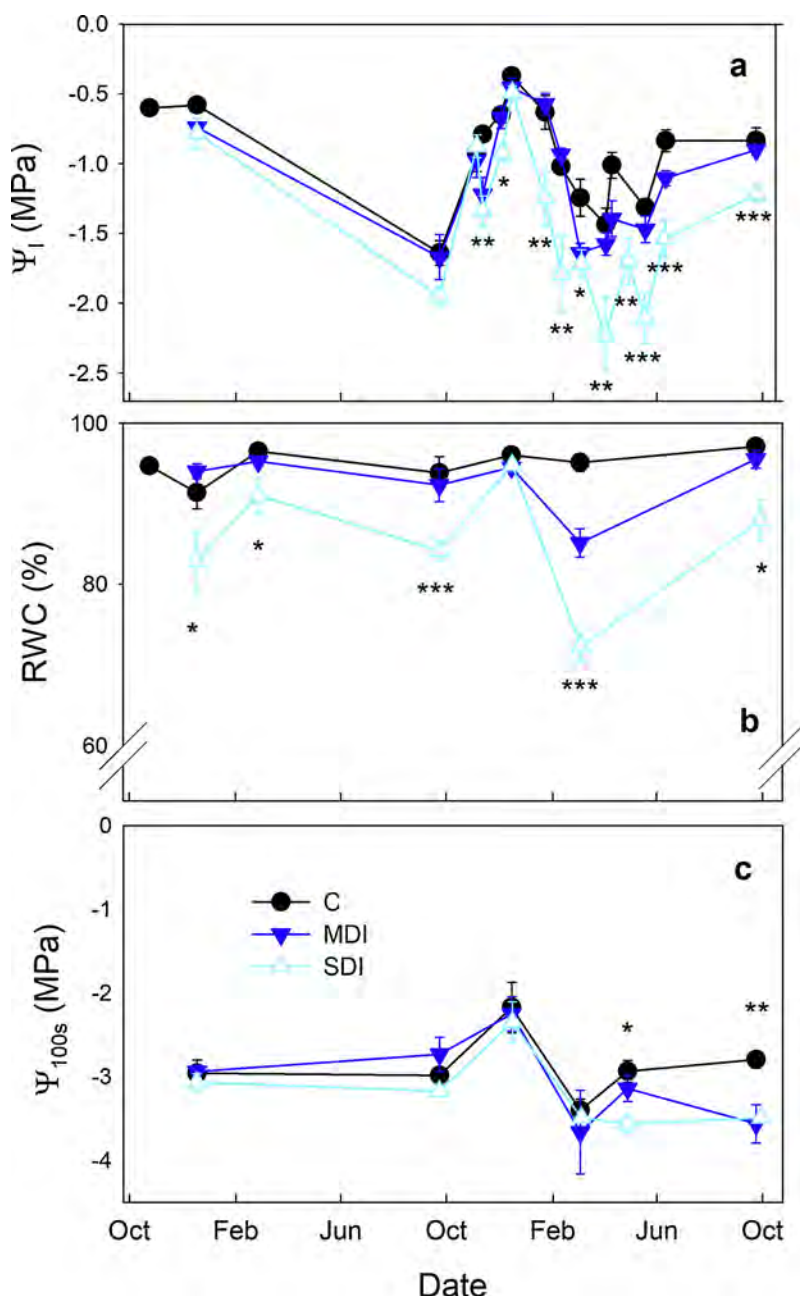
Fig. 2. Evolution of the leaf water potential (Ψ_l, a), leaf relative water content (RWC, b) and leaf osmotic potential at full turgor (Ψ_{100s}, c) at midday in *Phillyrea angustifolia* plants submitted to different irrigation treatments. Values are the mean of seven plants, except in leaf osmotic potential at full turgor, when values are the mean of five plants. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (*P < 0.05, **P < 0.01, ***P < 0.001).

transplanting), Ψ_l remained lower in SDI plants than in the control and MDI plants.

RWC values showed a similar behaviour to that observed for Ψ_l, with SDI plants having the lowest values, especially in spring (March) (Fig. 2B). This was followed by an increase in the values of RWC for water deficit treatments until the end of the summer, when significant differences with the control were only observed in SDI (23 months after transplanting). No pronounced differences in RWC were observed between control and MDI during most of the experimental period, although MDI affected RWC during spring (March), when lower values were observed in the MDI treatment compared with the control (Fig. 2B).

In general, the plants subjected to both water deficit treatments showed lower stomatal conductance than the control, especially in the

case of severe water stress (Fig. 3A). Such reductions with respect to the control plants were also observed in the P_n levels in both water stress treatments (Fig. 3B). The seasonal pattern of g_s consisted of a spring depression in all treatments as the evaporative demand of the atmosphere increased (15–18 months). Regardless of the amount of water applied, all the plants had very low values of below 50 µmmol m^{-2}s^{-1} at the end of spring (18 months), although plants of the SDI treatment also reached very low g_s values during the previous 3 months. These lower values of g_s and P_n recorded in spring were followed by a marked increase in all irrigation treatments until the end of summer. At the end of the experiment (September), plants from both deficit irrigation treatments had similar g_s values to control plants and even higher P_n values than the control plants, meaning that intrinsic water use efficiency P_n/g_s increased in the deficit irrigation plants at this time.
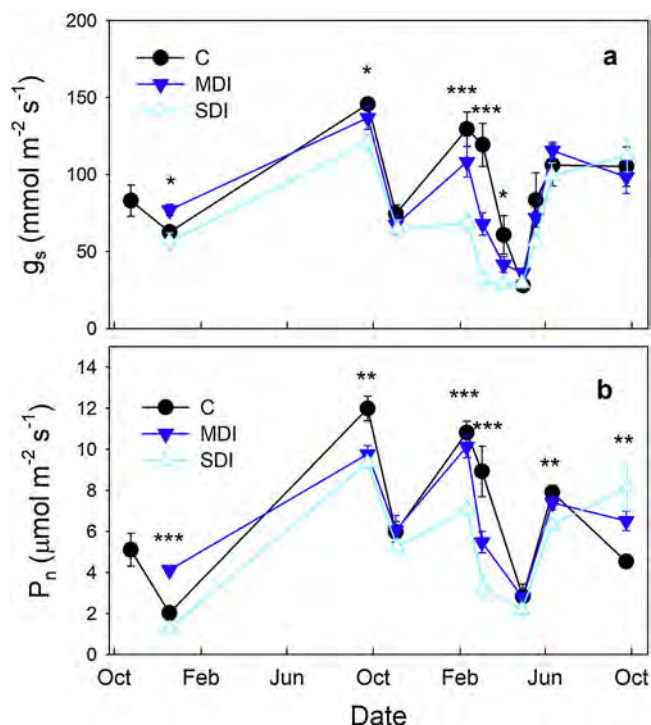
Fig. 3. Evolution of stomatal conductance (g_s; a) and net photosynthetic rate (P_n; b) in *Phillyrea angustifolia* plants submitted to different irrigation treatments. Values are means s.e., n = 7. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (*P < 0.05, **P < 0.01, ***P < 0.001).

Fig. 4. Evolution of chlorophyll fluorescence values (F_v/F_m; a) and relative chlorophyll content (RCC, b) in *Phillyrea angustifolia* plants submitted to different irrigation treatments. Values are the mean of 20 plants in RCC and values are the mean of 5 plants in F_v/F_m. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (*P < 0.05, ***P < 0.001).

Leaf osmotic potential values at full turgor (Ψ_{100s}) decreased in all deficit irrigation treatments, which was indicative of the osmotic adjustment that occurred due to deficit irrigation. The difference between the values obtained in the control and stressed plants were taken as an estimate of this adjustment, 0.76 and 0.70 MPa for MDI and SDI respectively (Fig. 2C).

The chlorophyll fluorescence values (F_v/F_m) did not change in any of the treatments during the experiment, remaining at around 0.75 − 0.80 (Fig. 4A). Membrane damage, assessed by ion leakage was not affected by the water availability conditions of the substrate (Table 1).

3.2. Plant growth and ornamental parameters

Water deficit affected the growth and size of the *Phillyrea angustifolia* plants (Table 1). Plants submitted to severe deficit irrigation (SDI) showed a reduction in biomass production at the end of the experimental period although no significant differences were observed between moderate deficit irrigation (MDI) and control treatments (Table 1). At the end of the experiment, SDI plants showed reduced leaf dry weight (DW) compared with the control, whereas the stem and root DW were not affected by the water availability conditions in the substrate. Plants submitted to severe deficit irrigation treatment showed an increase in the root to shoot ratio and the specific leaf area (SLA) at the end of the experimental period, while these parameters were not modified in plant submitted to MDI. Succulence did not change in any of the treatments.

The irrigation regime also affected plant height and differences between treatments were evident throughout the experimental period in this respect. Plant height was significantly reduced by both water deficit treatments 21 months after application of the deficit irrigation onwards (Fig. 5A), with reductions of 18 and 21% for MDI and SDI,
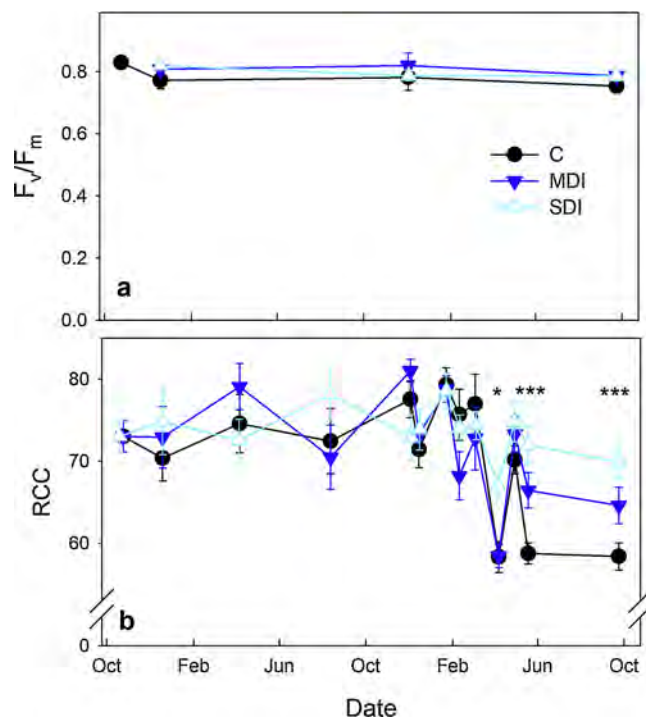
respectively, compared with the control at the end of the experiment. Water deficit also led to a decrease in the relative growth rate as a function of plant height (RGR) during spring, the reductions being more marked in the severe deficit irrigation and in the second growth season (15–18 months after transplanting) (Fig. 5B).

In both deficit irrigation treatments, plant height and leaf area were reduced to a similar extent compared with the control, with the result that compactness was not modified in these plants (Table 1). Water deficit led to an increase in water use efficiency (WUE) in all parts of the plant (leaf, stem and root), but this increase was only significant in roots of the severe water deficit plants (Fig. 6).

No differences in the leaf colour parameters (lightness, chroma and hue angle) were observed in MDI compared with the control (Fig. 7). The higher h° and RCC values and lower C* values recorded in the leaves of the plants submitted to SDI at the end of the experiment confirmed the darker and less vivid green colour of the foliage compared with control plants (Figs. 7B-C and 4 B).

4. Discussion

Common responses in species exposed to saline or drought stress are an increase in osmotic adjustment and changes in cell wall elasticity, which result in the turgor loss point being reached at a lower leaf water potential and at a lower relative water content (Navarro et al., 2009; Suárez, 2011; Álvarez and Sánchez-Blanco, 2015). In our assay, at the end of the experimental period, *P. angustifolia* plants exposed to water stress showed osmotic adjustment as a tolerance mechanism to drought in order to maintain turgor, facilitating the continued uptake of water from the soil. Similar results have also been reported in many other ornamental species, such as Callistemon, a woody plant (Álvarez et al., 2011; Álvarez and Sánchez-Blanco, 2015) or in geranium and carnation, herbaceous plants (Sánchez-Blanco et al., 2009; Álvarez et al.,

Table 1

Growth parameters and ion leakage at the end of the experiment in *Phillyrea angustifolia* subjected to different irrigation treatments. Values are the mean of eight plants, except in ion leakage, where values are the mean of five plants.

Parameter	C				MDI				SDI				P
Leaf DW (g plant^{-1})	22.2	±	2.1	b	14.6	±	3.6	ab	11.9	±	2,1	a	*
Stem DW (g plant^{-1})	42.8	±	5.1		31.6	±	10.5		30.2	±	4.4		ns
Root DW (g plant^{-1})	24.8	±	3.4		23.8	±	4.6		22.2	±	3.8		ns
Root to shoot ratio	1.1	±	0.1	a	1.6	±	0.1	ab	1.9	±	0.2	b	*
SLA (cm^2 g^{-1})	56.5	±	4.4	a	55.8	±	5.0	a	74.4	±	3.8	b	*
Leaf succulence	2.16	±	0.11		2.13	±	0.08		2.30	±	0.07		ns
Leaf area (cm^2)	1172	±	138		861	±	162		1040	±	275		ns
Compactness (cm^2 cm^{-1})	20.5	±	3.3		19.8	±	2.9		22.8	±	3.7		ns
Ion leakage (%)	56.7	±	4.9		64.8	±	8.6		63.4	±	5.6		ns

Means within a row without a common letter are significantly different according to Duncan 0.05 test.
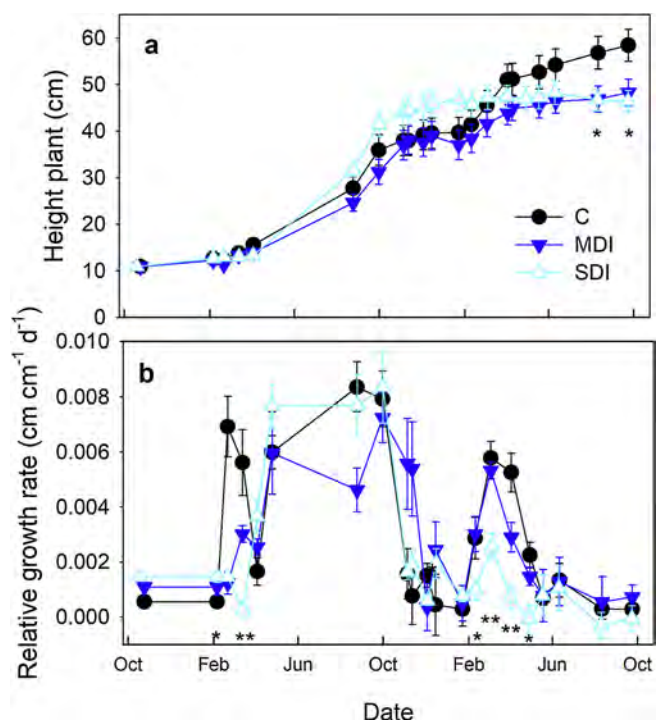(P; probability level, ns; non significance, *P < 0.05, ** P ≤ 0.01, *** P ≤ 0.001).

Fig. 5. Evolution of plant height (a) and relative growth rate of height (b) in *Phillyrea angustifolia* plants submitted to different irrigation treatments. Values are means s.e., n = 25. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (*P < 0.05, **P < 0.01).

Fig. 6. Water use efficiency of production (WUE) at the end of the experimental period in *P. angustifolia* plants submitted to different irrigation treatments. Values are means s.e., n = 8. Means within a part of the plant without a common letter are significantly different by Duncan$_{0.05 \text{ test}}$.

2009). However, Álvarez et al. (2018) found that *Pistacia lentiscus* plants did not show osmotic adjustment in the face of water stress and, in this case, turgor maintenance was associated with increases in cell wall elasticity (decreases in ε, tissues more elastic). Long periods of water stress can produce significant modifications in the morphofunctional characteristics of plants, as if a preconditioning process had occurred during the experiment (Rubio et al., 2001). Previous studies in *Pistacia lentiscus* showed that this species is very sensitive to preconditioning and one of the modifications related to this process (acclimation) is the higher elasticity of cell membranes (Álvarez et al., 2018).

The maintenance of turgor through the passive concentration of solutes (increased solute concentration as a result of reduced cell volume) under drought stress is an advantageous mechanism in arid environments to avoid energetic costs a result of the synthesis of organic solutes (Evans et al., 1992; Sucre and Suárez, 2011; Acosta-Motos et al., 2017). Under water stress, increased succulence may dilute organic ion
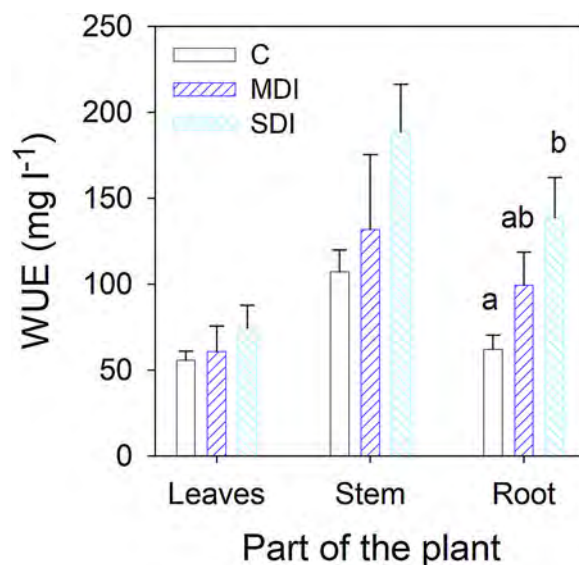
concentration, increasing the cost of osmotic adjustment (Flowers and Yeo, 1986; Sucre and Suárez, 2011), which did not occur in our assay, as succulence was not affected by either water stress level.

As regards water status, plants exposed to deficit irrigation exhibited slight dehydration throughout the experiment, especially in spring, as indicated by the lower Ψ$_l$ and RWC, due to the low availability of the substrate water (Remorini and Massai, 2003).The increasing evaporative demand during spring decreased the leaf water potential and the lowest Ψ$_l$ values for C, MDI and SDI plants were reached in April (between −1.1 and −2.2 MPa). The diurnal course in Ψ$_l$ reflected the stress conditions and even the watered plants were mildly stressed, which may have been the consequence of high air temperature and irradiance producing low Ψ$_l$ and stomatal conductance at midday (Bacelar et al., 2007; Gratani et al., 2013). However, as water stress progressed over time, a process of acclimation to drought could have occurred in these plants, which was reflected in the subsequent recovery that occurred in *P. angustifolia* during summer (19–23 months after transplanting), with values of Ψ$_l$ and RWC that were higher than those previously obtained. These changes, together with the osmotic adjustment reached at the end of the experiment, allowed deficit irrigation plants to maintain relatively high net photosynthetic rates and a high photosystem II status, and these plants only showed slight growth reduction, suggesting that acclimation to drought thorough changes in water relations (Vilagrosa et al., 2003; Sucre and
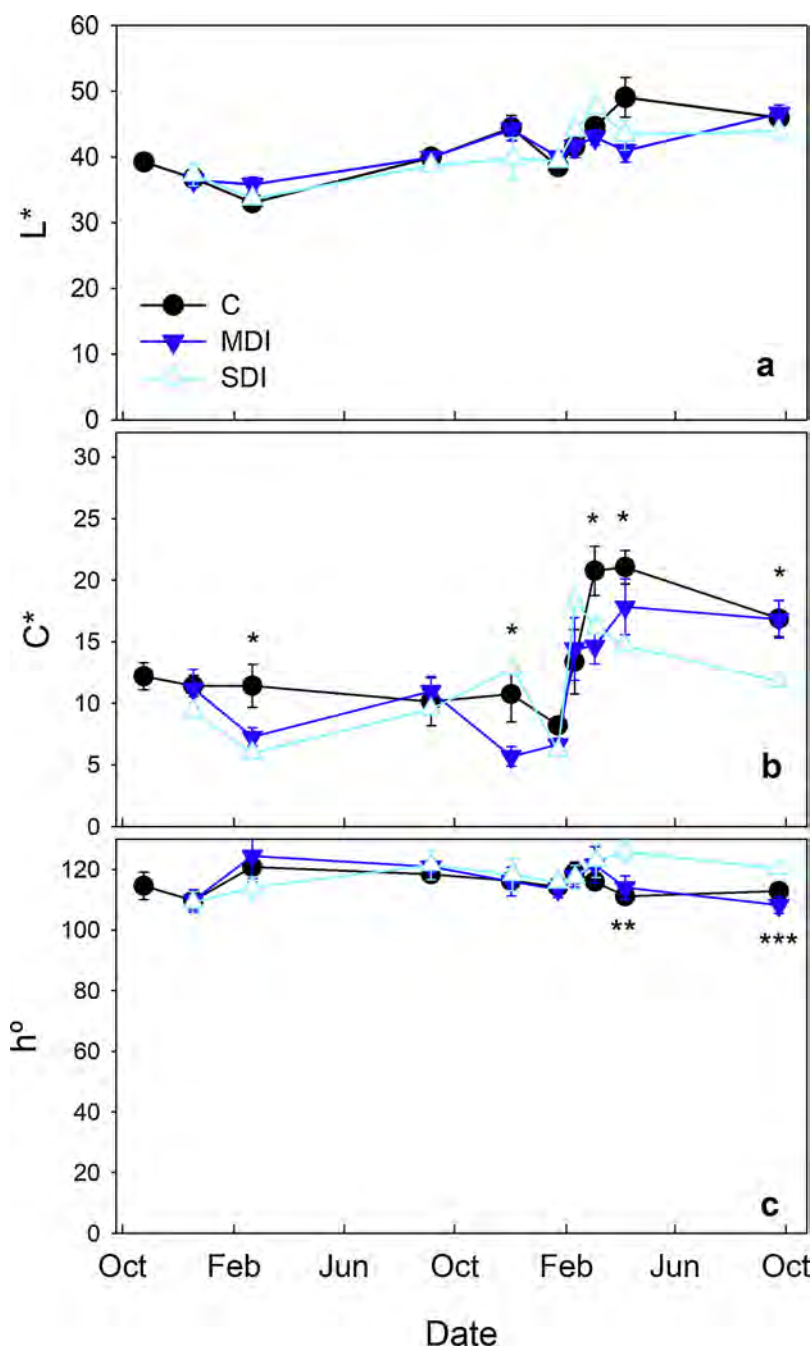
Fig. 7. Evolution of leaf color parameters, Lightness (L*; a), Chroma (C*; b) and hue angle (h°, c) in *P.angustifolia* plants submitted to different irrigation treatments. Values are means s.e., n = 8. Symbols represent the different treatments: Control (filled circles), moderate deficit irrigation (filled triangles) and severe deficit irrigation (open triangles). For each studied day, asterisks indicate significantly different between treatments (*P < 0.05, **P < 0.01, ***P < 0.001).

Suárez, 2011). In addition, as indicated in the results, P_n/g_s and WUE was higher in *P. angustifolia* plants growing in severe deficit irrigation conditions (SDI), a response that has been observed in numerous ornamental plants (Cameron et al., 2006; Jaleel et al., 2008; Mugnai et al., 2009; Álvarez et al., 2009, 2012; 2018). Unlike in agriculture, improving WUE in the urban landscape does not necessarily mean improving the overall yield or growth. The ultimate goal is rather to achieve a more efficient use of water accompanied by suitable aesthetic appearance and plant fitness (Stabler and Martin, 2000). Our estimation of higher WUE under lower irrigation conditions agreed with those of Nazemi Rafi et al. (2019a), who observed *Althae rosea* and *Rudbeckia hirta* (ornamental herbaceous plants) under deficit irrigation had higher thickness, better light interception (Chaves et al., 2002), the presence of

trichomes (Dunkić et al., 2001) and decreased leaf area (Lazaridou and Koutroubas, 2004; Huang et al., 2005), which may have led to a better water saving and an improvement in WUE. Therefore, WUE could be considered as an index of the ability of the plant species to save water under dry conditions (Fang et al., 2010).

Plant functioning and gas exchange attributes were affected by water deprivation, as lower P_n and g_s values were observed under DI treatments, especially in spring, when environmental conditions were more stressful. This indicates that *P. angustifolia* plants regulated their transpiration when subjected to water constraints (Ruiz-Sánchez et al., 2010), which is a common response of cultivated and ornamental plants grown in Mediterranean climates (Grant et al., 2012; Toscano et al., 2019).

Photosynthetic reductions are strongly associated to stomatal closure and consequent decreases of intracellular CO_2 (Morales et al., 2008). In addition, the analysis of chlorophyll fluorescence rates supports the idea that stomatal factors were the main factor responsible for the decline in photosynthesis observed in our experiment. In this sense, the absence of any change or difference in the F_v/F_m ratio in *P. angustifolia* during the experiment suggests that severe drought did not cause damage to leaf tissue, or, at least, it was not irreversible, indicating that the maximal PSII primary photochemistry was not permanently affected by the stressful conditions experienced by the plants. In a similar way, Peñuelas et al. (2004) observed that *P. angustifolia* leaves can avoid damage to the photosynthetic apparatus by changing pigment and antioxidant levels in response to drought-induced oxidative stress, and the dissipation of excess excitation energy seems to afford protection to the photosynthetic apparatus in drought-stressed *P. angustifolia* plants. Thus, this species did not suffer from photoinhibitory damage to its photosynthetic apparatus (as indicated by the absence of significant changes in F_v/F_m and MDA levels), at least at the drought stress levels tested by Peñuelas (RWCs above 50%), although it may occur later, when stress is more severe. In the present study, this level of stress was not reached for plants at any sampling time during the experiment and RWC values were always higher than 70%.

Moreover, the increases in leaf RCC in *P. angustifolia* plants subjected to water stress during the experimental period suggest that there was no oxidative damage. In this sense, chloroplasts in Mediterranean species under drought and high light conditions have been shown to possess several strategies to avoid photoinhibitory processes, e.g., mechanisms to consume the reducing power generated by PSII (Flexas and Medrano, 2002; Demmig-Adams and Adams, 2006).

These results agree with those of Vilagrosa et al. (2010), who reported high resistance at chloroplast level for *P. lentiscus* under drought conditions. Additionally, our data about the unchanged (not decreased) leaf chlorophyll content in drought stressed plants are consistent with the previous study of Peñuelas et al. (2004) in *P. angustifolia*, who reported that this species is able to activate several mechanisms of photo- and antioxidant protection to withstand drought stress during the Mediterranean summer. In addition, when the drought is not extremely severe, these mechanisms are able to protect the tissues from lipid peroxidation, and to allow the maintenance of high photosynthetic rates if meteorological conditions are adequate.

Drought is one of the most important environmental stresses limiting plant establishment and growth (Cregg, 2002; Fang et al., 2010; Ali et al., 2017). While the prime effect of water stress in agricultural crops is yield reduction, the most important drought stress effects in ornamental plants are negative effects on their visual quality and decorative effect (Cirillo et al., 2014; Caser et al., 2017; Nazemi Rafi et al., 2019a). Responses to drought stress have been widely reported in different ornamental species and one of the consequences of exposing plants to a reduced water supply in terms of plant growth is the lower biomass accumulation, the production of smaller leaves and reductions in size and/or quality (Sánchez-Blanco et al., 2002; Franco et al., 2006; Andrew et al., 2013). The different levels of irrigation applied in our assay led to substantial differences in the growth of *P. angustifolia* plants. While moderate water stress produced no significant changes in plant development (with the exception of plant height), a greater water deficit clearly reduced the aerial growth parameters. This finding may be important for growers because ornamental plants are often exposed to drought treatments during nursery production to reduce excessive vigour and promote a more compact habit without applying growth retardants. However, it goes without saying that it is first necessary to know the severity of the water stress to which a species can be exposed to maintain healthy growth without reducing quality (Henson et al., 2006; Cirillo et al., 2017).

Although by the end of experiment water stress had inhibited the size of *P. angustifolia*, such a reduction was only noticeable long after the beginning of the treatments, confirming that the duration of the stress is also an important factor. The highest drought stress level clearly induced the lowest growth rates, especially during spring, when the evaporative demand of the atmosphere increased. Similar to other woody perennials in arid zones, *P. angustifolia* is slow growing, even with an optimal water supply and nutrient availability (mean RGR was lower than 0.01 d^{-1} for our control plants), as previously reported for *Phillyrea latifolia* (Tattini et al., 2002).

In our conditions, deficit irrigation did not increase the relationship between leaf area and plant height. However, importantly, it did not decreased either, so that the ornamental value of the plants was maintained. In this study, visual appeal was mainly affected by the severe deficit irrigation treatment, which leds to plants with lower leaf growth and leaves of a less intense color, which would have decreased the commercial value of these plants destined for decorative purposes. The response of species to stresses in terms of growth is the ultimate expression of several interacting physiological and biochemical parameters and has often been used to characterise salt or water deficit tolerance (Sidari et al., 2008; Cassaniti et al., 2009). However, the absence of reductions in growth during stress does not necessarily guarantee adequate aesthetic values (Nazemi Rafi et al., 2019a), as high visual quality also depends on other characteristics, such as foliage colour, or the absence of symptoms of necrosis. Moreover, aesthetically and commercially, an increase in foliage size in relation to plant height gives the plant a compactness and architectural equilibrium that are much appreciated by customers (Álvarez et al., 2013). Deficit irrigation has the potential to improve crop quality by promoting a more compact habit, as previously reported for other ornamental species (Álvarez et al., 2009).

As regards biomass partitioning, drought exposed plants in our study reduced their aerial growth more than root growth, resulting in an increased root to shoot ratio, although this only occurred in SDI plants, confirming the importance of the severity of the water stress. These responses have been described in several ornamental species by Jaleel et al. (2008) in *Catharanthus roseus*, by Henson et al. (2006) and by Hassanein and Dorion (2006) in *P. hortorum*, by Andersson (2001) in *Pelargonium zonale*, by Andersson (2011) in *I. walleriana* and *Petunia* x *hybrid* and by Nazemi Rafi et al. (2019a) in *Althaea rosea*. Nevertheless, this ratio is not always increased by drought stress. Álvarez et al. (2018) reported that the root to shoot ratio in *Pistacia lentiscus* was not affected under drought conditions and Navarro et al. (2009) mentioned that severe water deficit similar to that used in our trial significantly reduced the root to shoot ratio in *Myrtus* plants. The attractiveness and commercial value of ornamental plants destined for use in gardens is associated with visual appeal, such as high intensity and duration of flowering, adequate development, leaves of intense colour and an acceptable relationship between plant height and leaf area (Álvarez et al., 2013; Carillo et al., 2019). However, when plants are used for landscaping and revegetation purposes, the nursery industry values plants with a high root to shoot ratio, increased water use efficiency and an improved root system (Franco et al., 2006; Álvarez and Sánchez-Blanco, 2015). This last aspect is an important factor for successful transplanting and establishment in the field, since root anatomy and structure may be decisive for plant survival (Bañón et al., 2004).

The slight inhibition of leaf growth as a result of the severe water deficit is seen as an adaptation, because it allows plants to avoid large water losses by lowering transpiration and delaying the onset of more severe stress (De Herralde et al., 1998; Ruiz-Sánchez et al., 2000; Bañón et al., 2006). In this sense, severe deficit irrigation in nursery conditions would improve resistance to water deficit situations when plants grow in field conditions after transplanting (Franco et al., 2006). This was confirmed by the increased root to shoot ratio and the proportion of plant biomass invested in leaf area (SLA) as a result of the severe water deficit, which confer and advantage in resource-uptake efficiency, by increasing the absorption surface per unit of tissue biomass and may be decisive for plant survival (de la Riva et al., 2016; Álvarez et al., 2018). Despite being a morphological trait, SLA is widely used as a good

indicator of plant functioning, not only for the prediction of drought tolerance, but also for competitive effects in landscape planting, as it is highly correlated with processes such as photosynthetic capacity, potential growth rate, chemical composition and resistance to herbivory (Nazemi Rafi et al., 2019a). In our conditions, the highest water use efficiency of production (WUE) estimated as dry weight per unit of water used, together with an increased root to shoot ratio could promote a more rapid establishment in landscape conditions.

5. Conclusion

In conclusion, our results showed that using deficit irrigation in *P. angustifolia* under Mediterranean conditions is a viable irrigation management strategy forsaving water without compromising the overall quality of the ornamental plants. The tolerance of *P. angustifolia* to drought was related to a slight osmotic adjustment and an effective mechanism of stomatal control. The results show that *P. angustifolia* is highly resistant to water stress, but the morphological and physiological responses differed between both deficit irrigation levels. In this sense, moderate deficit irrigation, MDI involvingreductions of 40% of the water supplied, did not affect aesthetic features (biomass accumulation, compactness and leaf color) in *P. angustifolia* plants, which may be of interest for optimizing sustainable high-quality production. However, reductions of 60% of the water applied (severe deficit irrigation, SDI) inhibited plant growth, but was accompanied by an increased root to shoot and water use efficiency, which are positive aspects that would allow the plants to overcome the transplant shock that can occur later in landscaping projects. Based on its observed behaviour, *P. angustifolia* can be regarded as an interesting ornamental species for gardening and landscaping projects in arid areas.

Acknowledgements

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