

HYDRAULIC RELATIONS AND WATER USE OF MEDITERRANEAN ORNAMENTAL SHRUBS IN CONTAINERS

Paolo ZUCCARINI^{1*}, Alejandro GALINDO², Arturo TORRECILLAS³,
Alberto PARDOSSI⁴, Brent CLOTHIER⁵

¹ CSIC, Global Ecology Unit CREAM-CEAB-UAB, Cerdanyola del Vallès, 08193 Catalonia, Spain

² Department of Agroforestry Science, Universidad de Sevilla, 41013, Sevilla, Spain

³ Department of Plant Sciences and Microbiology, Escuela Politécnica Superior de Orihuela, 03312, Alicante, Spain

⁴ Dipartimento di Scienze Agrarie, Alimentari e Agroambientali. University of Pisa, Pisa, Italy

⁵ Plant & Food Research, Batchelar Road, Palmerston North 4442, New Zealand

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ABSTRACT

A detailed, species-specific comprehension of plant water behavior can be a central tool to improve water management in nursery production and irrigated landscapes. Potted plants of *Nerium oleander*, *Pittosporum tobira*, and *Ligustrum japonicum* ‘Texanum’ were exposed to controlled increasing drought conditions in greenhouse. Water use, gas exchange, and foliar thermoregulation were monitored along the trial. *N. oleander* showed the most efficient response to increasing water stress, maintaining high levels of gas exchange and evapotranspiration rate during the whole trial, whereas *L. japonicum* emerged as the most sensitive species, with a significant drop in physiological performances already from the second day. The more aggressive water behavior of *N. oleander* can be compared to the one of anisohydric plants, whereas *L. japonicum* displays an isohydric strategy. *P. tobira* showed intermediate characteristics between the two other species. This work comes to provide useful tools for the management of irrigation in plant nursery and for decision making in the use of ornamental shrubs for landscape applications.

Key words: gas exchange, hydric behavior, Mediterranean shrubs, water stress, water use

Abbreviations: ET – evapotranspiration (mm); ETE_h – hourly evapotranspiration (mm·h⁻¹); gs – leaf stomatal conductance (mol·m⁻²·s⁻¹) (where gs_{por} = measured values and gs_{cal} = calculated values); RG – incident radiation (MJ·m⁻²·h⁻¹); VPD – vapor pressure deficit (kPa); C.C. – container capacity (%); ET/RG (g·MJ⁻¹)

INTRODUCTION

Agriculture is the largest consumer of water globally, accounting for 70% of total withdrawals (UNEP 2007) but is limited by shortfalls in water quality and quantity (Hoekstra & Chapagain 2007; Postel 2000). Limited water supplies, and continued population growth, demand more efficient water management (Sample 2009; IEEE 2010).

Demand for ornamental plants has been significantly increasing during the past decade (Incrocci et al. 2014) for purposes of urban decoration and gardening and also for environmental restoration and bioremediation (Denys et al. 2006; Sun et al. 2011). This fact, in combination with the above-mentioned aspects, implies a double challenge for the plant nursery industry, which will have to increase its production (Savé et al. 1999) and, at the

*Corresponding author:
e-mail: p.zuccarini@creaf.uab.cat

same time, reduce its water inputs through resource optimization.

Historically, one of the most important innovations in the nursery sector has been the switch from mineral soil to soilless cultivation in plastic containers filled with inert substrate that simplified the task of controlling and optimizing water inputs (Di Lorenzo et al. 2013). However, nursery stock in organic substrates are still over-irrigated and leach slow-release fertilizers (Ristvey et al. 2004), which wastes water and pollutes waterways (Stewart-Wade 2011).

Appropriate nursery irrigation requires scheduling in order to provide plants with the adequate amount of water at the correct time. Such scheduling can be based on (1) climate – the evaporative demand and its effects on soil–water balance; see Allen et al. (1998); (2) substrate – its water-holding properties, and the monitoring of substrate moisture (Θ) status; (3) plant water use traits – centered on the relationship between crop water stress and soil water deficit; see Jones (2004) or on their integration. In particular, mathematical modeling is a way to combine the abovementioned strategies with an integrated approach (Gu et al. 2020).

Although microclimate and substrate water-holding properties are quantifiable, plant water use traits are complex and vary among species and cultivars (Knox 1989; Schuch & Burger 1997; Mugnai et al. 1999). Few guidelines are nowadays available for the planning and management of irrigation, and in the reality of nursery production, these topics are addressed most of the times based on the empirical observations more than on modeling (Di Lorenzo et al. 2013).

The aim of the present work was to study the behavior of three ornamental species in containers under increasing water stress, through a continuous monitoring of their ecophysiological responses. The final aim is to highlight differences among the studied species and classify them based on their strategies of stress response, in order to optimize water investments and nursery practices according to the plant type.

MATERIALS AND METHODS

Experimental design

Three common ornamental shrubs were chosen for this experiment: *Nerium oleander* L., *Pittosporum tobira* Thunb., and *Ligustrum japonicum* Thunb. ‘Texanum’.

Plants, 14 months of age, were cultivated in plastic containers, with a 18-cm top diameter, 6.5 dm³ of volume, filled with a peat–pumice (1 : 1, v : v) mixture, and placed in a non-heated iron/PVC greenhouse, whose coordinates were 43°70'43" North and 10°42'75" West; the period of the year was September.

A five-day dry-down cycle versus control was performed. Plants were watered daily by hand as a partial or total root zone refilling of water lost through evapotranspiration. Control plants were kept at the 100% of container capacity during the whole trial, whereas stressed plants were subjected to 90%, 80%, 70%, and 60% of container capacity along the study period. Six replicates were used for each species and water treatment combination. The entire cycle was replicated three times, subsequently, on new specimens not previously subjected to drought stress.

Measurements

Air temperature (T) and relative humidity (RH) in the greenhouse were constantly monitored with a data logger FT-105/RF-LCD (Econorma®, Trento, Italy). For each day of trial, the average value of three measurements corresponding to the hours of the day with highest radiation (11:30, 12:30, and 13:30) was calculated. Vapor pressure deficit (VPD) was calculated from T and RH for the same hours.

Incident radiation was measured using a pyranometer (Delta-T Devices, Burwell, England) connected to the data logger. Global incident radiation during the period of measurements of the physiological parameters was calculated daily as the difference between the cumulated radiation values at 14:00 and 11:00. Climatic data are presented in Figure 1.

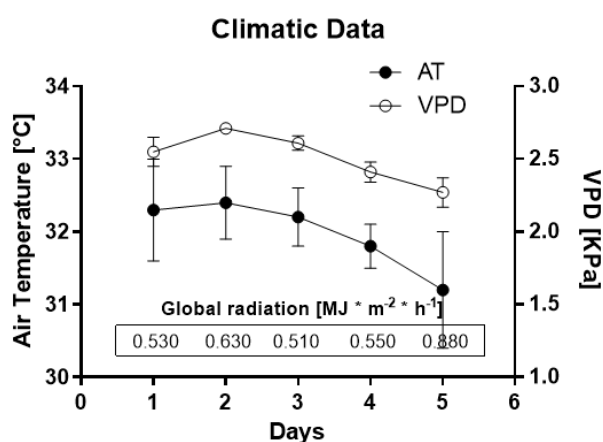


Fig. 1. Trend of climatic data during the days of experiment: Temperature (closed circles), vapor pressure deficit (VPD, open circles), and global radiation (RG) are shown. Error bars for each average value of temperature and VPD come from 3 measurements, taken at the hours of the day with highest radiation (11:30, 12:30, and 13:30). RG values refer to the interval 11:30–13:30

Water use was gravimetrically determined daily as the difference in weight between 14:00 (end of measurements) and 11:00 (beginning of measurements). Hourly evapotranspiration was then calculated.

Containers were weighted again every day at sunset in order to calculate the amount of water needed for the reintegration up to water content planned for the next day. A water retention curve was calculated for the substrate used in the experiment through tensiometric cassette and Richard's plates according to the Piemonte Region analytical methods (ARPA 1992; Cassel & Klute 1986). The relationships between container capacity and substrate water tension are given in Table 1.

Table 1. Substrate water tension (SWT) versus percentage of container capacity for the three investigated species

<i>N. oleander</i>		<i>L. japonicum</i>		<i>P. tobira</i>	
SWT	% C.C.	SWT	% C.C.	SWT	% C.C.
8	100	18	100	23	100
26	89.5	35	90.7	41	90.7
46	78.8	41	85.6	65	85.6
78	69.6	65	76.1	90	76.1
117	59.8	101	65.3	135	65.3

Leaf stomatal conductance was measured with a transit-time diffusion porometer (Mk3, Delta-T Devices, Burwell, England) and then transformed, for each species, into relative values ($gs_{rel} = [(gs_i/g_{s_{max}}) \cdot 100]$, where gs_i was one random measurement and gs_{max} was the maximum value recorded for a species.

Foliar temperature was measured through a portable infrared thermometer (Cyclops Compac 3 Minolta/Land, Sheffield, UK), assuming an emissivity (ϵ) of 0.93 for plant tissues (Styles et al. 2002). Both leaf conductance and temperature were measured daily on two marked leaves for each plant in the interval between 11:30 and 13:30.

At the end of the trial, the leaf area was measured for each plant with a digital planimeter (ΔT Area Meter Mk2, Delta-T Devices, Burwell, England).

Statistical analyses

Data were subjected to analysis of variance (ANOVA) using SAS version 9.1 (SAS Institute, USA). 3-way ANOVA was performed with species \times day (container water capacity) \times cycle as descriptors. The significance of differences between means was determined using Duncan's multiple range test (SAS 1990).

For each measurement of leaf stomatal conductance (gs_{por}), the corresponding modeled value gs_{cal} was calculated from the transpiration rate and VPD following the equation of Pearcy et al. (1991):

$$gs_{cal} = \frac{E \left\{ 1 - \left[\frac{(w_i - w_a)}{2} \right] \right\}}{w_i - w_a},$$

where: E is the transpiration rate as a function of ETE/RG ratio and foliar area and w_i and w_a are the values of partial vapor pressure (kPa) in the leaf intercellular spaces and in the atmosphere, respectively. Linear correlation was then performed separately for each species between gs_{por} and gs_{cal} values.

ANOVA of the eco-physiological plant variables (ET/RG, gs , and ΔT) showed no significant differences among cycles ($p > 0.05$) and no significant interaction between cycle and the two other factors (day and species). Therefore, data from the first cycle are presented here to show the trends of ET/RG, gs , and ΔT , as representative of the three cycle repetitions. The decrease in container water capacity in treated plants is expressed as the substrate water tension.

RESULTS

N. oleander showed lower leaf area per plant than the two other species (Fig. 2). ETE_h was heavily influenced by the amount of solar radiation. Owing to this reason, water use was calculated as ET/RG, which is the ratio between the total evapotranspiration along the three hours of measurement and the total amount of incident radiation during the same time (Fig. 3). All species displayed a clear trend toward ET/RG reduction as soil water tension increases, with *N. oleander* always showing significantly higher values than the other two species. *P. tobira* showed intermediate values, and *L. japonicum* showed the lowest ones. *N. oleander* and *P. tobira* showed a gradual decrease along the 5 days, whereas *L. japonicum* remarkably dropped down from the second day, undergoing a gradual further decrease in the remaining days.

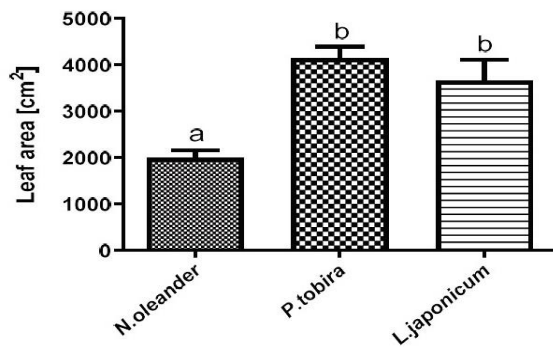


Fig. 2. Leaf area by species. Values marked with the same letter are not statistically different at $p < 0.05$, according to Duncan's multiple range test. Error bars were calculated from six measurements (replicates) for each average value

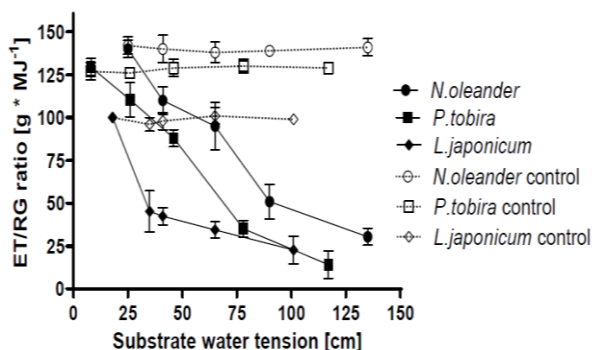


Fig. 3. ET/RG ratio versus substrate water tension
Note: See Fig. 2

Stomatal conductance declined for all species as soil water availability diminished (Fig. 4), whereas control plants kept their values at $100\% \pm 5\%$ (which means an average fluctuation of $\pm 5\%$ around the first-day-optimal value) during the whole trial (data not shown in the graph). For all the days of experiment, *N. oleander* showed the highest g_s values, followed by *P. tobira* and *L. japonicum*; g_s for *N. oleander* drastically dropped down only at the last day of trial, whereas *P. tobira* showed a gradual reduction and *L. japonicum* dropped down already between day 2 and day 3. The differences in stomatal conductance among plants were significant at 95% for all species in all days, except some overlapping between *P. tobira* and *L. japonicum* during the first 2 days. On the last day, following the dramatic drop of *N. oleander*, its values became comparable with the ones of *P. tobira* (Fig. 4). The high level of correlation obtained between the measured g_s values and the calculated ones confirms the reliability of the measured data. Three different correlation curves, one for each species, have been identified. The correlation curve for *L. japonicum* meets the origin of axes, with a slope close to one; *N. oleander* has a similar slope but all the measured values are higher than expected; *P. tobira* displays a markedly lower slope (Fig. 5).

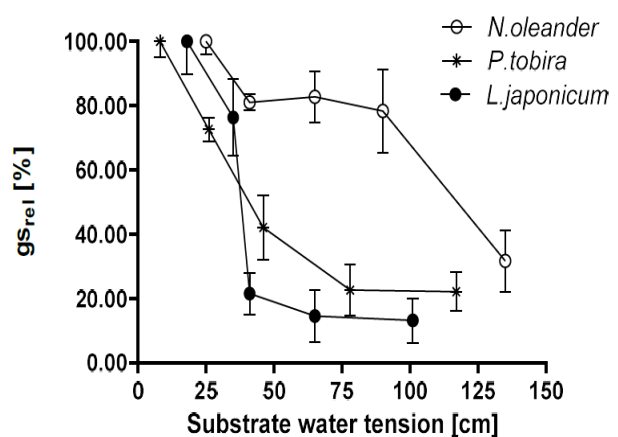


Fig. 4. Relative stomatal conductance ($g_{s_{rel}}$) versus substrate water tension
Note: See Fig. 2

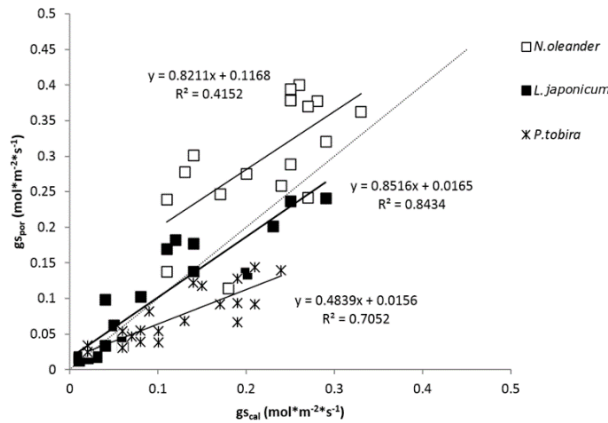


Fig. 5. Linear correlation between measured and calculated stomatal conductance; for each species, a single regression line, with slope and R², is presented in the graph; the central dotted line represents the ideal 1 : 1 relationship between measured and calculated g_s

ΔT ($T_{leaf} - T_{atm}$) increased for all species as water stress got more severe (Fig. 6), whereas control plants kept stable values (data not shown in the graph). *N.oleander* always showed the significantly lowest values, whereas the other two species had higher and similar values, with *L.japonicum* showing slightly higher ones. The difference between *N.oleander* and the other two species was significant at 95% during the first 4 days, whereas *P.tobira* and *L.japonicum* had values of ΔT that were more closely associated, even if those of *L.japonicum* always exceeded the ones of *P.tobira*.

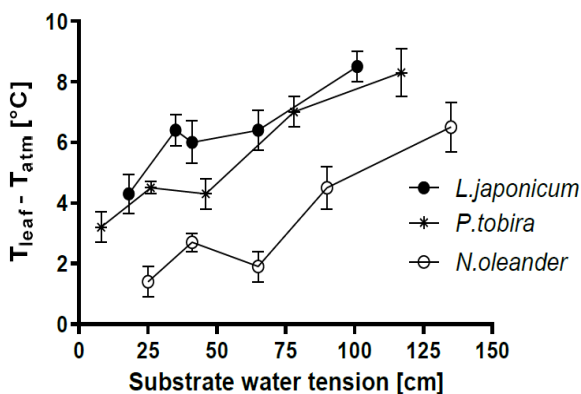


Fig. 6. ΔT versus substrate water tension. Note: See Fig. 2

DISCUSSION

The results point out *N.oleander* as the Mediterranean shrub displaying the greatest tolerance to conditions of increasing water stress. The values of evapotranspiration for *N.oleander* stay at the highest levels during all the stress period, possibly because of the lower leaf area and its different foliar architecture (Badger et al. 1982; Reinert et al. 2013). In fact, *N.oleander* shows a more markedly vertical leaf habit than the other two species, resulting in a lower mutual shading of its leaves, partially counterbalanced by a sharper angle of solar incidence. Moreover, the lower leaf area index of *N.oleander* is likely to be associated with a higher contribution of evaporation from the substrate to the total evapotranspiration (Allen 1998; Yan et al. 2012).

This phenomenon is also explained by the capacity of *N.oleander* of maintaining higher levels of stomatal gas exchange despite the increasing drought conditions. In fact, absolute g_s values of *N.oleander* were the highest during the whole trial, even on the last day when they decreased sharply, consistent with the observations of Mugnai et al. (1999). Relative g_s values show an even stronger trend, because, at the end of the trial, *N.oleander* stays at a 40% of its maximum gas exchange capacity, whereas the other two species drop down to a 20% and earlier than *N.oleander*. Concurrent higher surface evaporation from *N.oleander* substrate, likely due to less shading from lower leaf area, apparently led to more negative substrate water tension increasing more rapidly over the study period, despite regular re-watering, than the other two species. Finally, linear correlation between measured and calculated g_s clearly shows that *N.oleander* systematically gives higher scores of stomatal conductance than the ones predicted by the equation.

The similar leaf areas for *P.tobira* and *L.japonicum* exclude that differences in evapotranspiration between the two may be due to significant differences in evaporation from the substrate.

The higher ETE/RG for *P. tobira*, therefore, suggests that it maintains higher levels of foliar transpiration than *L. japonicum* in conditions of water stress, which is precisely confirmed by the evolution of their g_s values along time. The greater sensitivity of *L. japonicum* to water stress may be due to two reasons: gas exchange levels starting initially from lower values, which decreases rapidly with water stress onset. These observations suggest a more isohydric behavior of *L. japonicum* toward drought: the stomata close as soon as the water stress starts to manifest. This behavior is associated with lower risks of hydraulic failure and also reduced gas exchange and carbon uptake and is typical of plants that are defined “drought avoiders” (Tardieu & Simonneau 1998).

On the other side, the hydraulic behavior of *N. oleander* suggests anisohydric behavior of ostensibly drought-tolerant plants, which maintain gas exchange at the cost of more negative internal water potentials and risk of hydraulic failure and embolisms (Sperry & Tyree 1988; Sade et al. 2012). For this reason, anisohydric plants usually have stronger vascular structures and better protoplasmic and biochemical stability (Demmig et al. 1988; Vilagrosa et al. 2010).

The increase in ΔT from day 1 to day 5 is a typical consequence of reduced foliar transpiration because of stomatal closure from water stress, which reduces evaporative cooling and so leaf temperature rises (Mugnai 2004; Zuccarini et al. 2011). Low $T_{\text{leaf}} - T_{\text{atm}}$ in *N. oleander* during the study indicates greater evaporative cooling from transpiration, which directly reflects its higher rates of stomatal transpiration in comparison with the other two species.

Few studies have reported on hydraulic behavior of *N. oleander*, *P. tobira*, and/or *L. japonicum* under water stress, and they were not focused on interspecific comparisons. In this sense, this work is among the few ones reporting on differences in hydraulic behavior among Mediterranean shrubs that can improve their water management in nursery production.

Björkman et al. (1980) already showed gas exchange rates of *N. oleander* decreased with water stress and suggested that effects of water stress and high irradiation may be interrelated, leading to inactivation of PSII (Björkman & Powles 1984). Later, Demmig et al. (1988) demonstrated in *N. oleander*, high capacity of its leaves to create foliar zeaxanthin under water and light stress, which protects photosystems from damage through promotion of radiation less dissipation of excess energy, possibly explaining greater drought tolerance in *N. oleander* and also from a biochemical point of view.

This study suggests that *N. oleander* tolerates greater drought stress through anisohydric behavior, which maintains gas exchange at lower substrate water potentials. *L. japonicum* conversely appears to show isohydric behavior in rapidly reducing gas exchange at the onset of water stress, whereas *P. tobira* has an intermediate response.

The present data point out *N. oleander* as the most efficient choice for landscape use in environments subject to recurring situations of water scarcity and, at the same time, they provide useful information for a more focused irrigation management of these Mediterranean shrubs for the plant nursery industry.

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