

# Responses of Growth and Photosynthesis in Potted *Radermachera hainanensis* and *R. sinica* to Various Medium Water Contents

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## Abstract

*Radermachera hainanensis* Merr. and *R. sinica* Hemsl. are woody ornamental plants commonly used for indoor or landscape purposes. However, there is currently a lack of information regarding their water management. Potted plants of these two species were subjected to four volumetric water content (VWC) treatments: 20% VWC (dry), 20%/60% VWC (dry/wet cycle), 40% VWC (moisture), and 70% VWC (waterlogging). Results revealed that both *Radermachera* species exhibited the poorest growth under the 20% VWC treatment, with the lowest stem diameter, leaf area, plant dry weight, net photosynthetic rate ( $P_n$ ), stomatal conductance, and maximum quantum efficiency of photosystem II (Fv/Fm). The maximum stem diameter, leaf area, and root dry weight were recorded with the 40% VWC treatment. Stem diameter, leaf area,  $P_n$ , and Fv/Fm were higher in both *Radermachera* species with the 20%/60% VWC compared to the 20% VWC treatment. *R. sinica* exposed to 20%/60% VWC exhibited similar root dry weight and leaf drop as those with the 40% VWC treatment, while *R. hainanensis* showed lower root dry weight and higher leaf drop compared to the 40% VWC. Root dry weight,  $P_n$ , and Fv/Fm remained unchanged in *R. sinica* but reduced in *R. hainanensis* with the 70% VWC compared to the 40% VWC.

**Species used in this study:** Golden jasmine tree, *Radermachera hainanensis* Merr.; China Doll, *Radermachera sinica* Hemsl.

**Index words:** drought, foliage plant, volumetric water content, water stress, waterlogging.

## Significance to the Horticulture Industry

Effective water management plays a crucial role in the production of potted plants. *Radermachera hainanensis* and *R. sinica* have been widely used as ornamental foliage plants or outdoor landscapes in tropical or subtropical regions. However, scientific reports on their irrigation are lacking. This research contributes valuable insights into water management by employing the WET (Water content/Electrical conductivity/Temperature) sensor to measure the effects of volumetric medium water content on photosynthesis and growth of these two *Radermachera* species. The results are expected to provide valuable guidance for nursery management of potted *Radermachera*. These two *Radermachera* species, characterized by various pinnate-compound leaves and varying leaflet sizes, could serve as a promising model for studying the fundamental aspects of hydraulic architecture, including water relationships, gas exchange, and their distribution across different habitats.

## Introduction

China Doll (*Radermachera sinica*) and *R. hainanensis* are woody ornamental plants belonging to the Bignoniaceae family and are native to the tropical Asian region. China Doll was introduced to Europe, America, and New Zealand in the 1980s and 1990s (Griffith 2006, Thomas et al. 1995). *Radermachera hainanensis* has recently been among the top ten ranked potted plants in Taiwan. China Doll has bipinnately to tripinnately compound leaves with elliptic or ovate leaflets [3-6 cm (1.18-2.36 in) length, 1-

2.5 cm (0.39-0.98 in) width] and sharply pointed tips. *Radermachera hainanensis* is characterized by pinnately or bipinnately compound leaves with ovate leaflets [5-10 cm (1.97-3.94 in) length, 3-5 cm (1.18-1.97 in) width] and gradually pointed leaf tips. Both species have dark green, glossy leaves and are widely used in many areas for landscaping and indoor decorations due to their ability to thrive in a broad range of light intensities.

In indoor conditions, China Doll demands higher irrigation amounts compared to other foliage plants such as Norfolk Island pine [*Araucaria heterophylla* (Salisb.) Franco], golden pothos [*Epipremnum aureum* (Linden & André) G.S.Bunting], dumb cane [*Dieffenbachia seguine* (Jacq.) Schott] 'Camilla', and Ming aralia [*Polyscias fruticosa* (L.) Harms] (Poole and Conover 1992). However, excessive moisture or waterlogging may result in ethylene production (Pan et al. 2021). Whether this affects ethylene-sensitive China Doll, probably leading to severe leaf drop (Dunlap et al. 1994), requires further investigation. Griffith (2006) suggested, based on production experience, that China Doll should not be cultivated in overly wet or dry growing media, but there is currently no research on the water management practices for *R. hainanensis* and *R. sinica*.

The impact of drought stress on the growth and photosynthesis of woody ornamental plants varies depending on the species/cultivar. Percival and Sheriffs (2002) successfully identified drought-tolerant woody perennials using chlorophyll fluorescence such as maximum photochemical quantum yield (Fv/Fm). Lantana (*Lantana camara* L.) and Chinese privet (*Ligustrum lucidum* W.T. Aiton) subjected to the 25% water container capacity (WCC, i.e., the water capacity in container growing medium) treatment exhibit reductions in dry weight, leaf area, net photosynthetic rate ( $P_n$ ), stomatal conductance ( $g_s$ ), and Fv/Fm compared to the 100% WCC treatment. The 25% WCC treatment reduced leaf number in lantana but did not affect number of leaves

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in Chinese privet (Toscano et al. 2018). In comparison to irrigation based on daily evapotranspiration (ET), the 25% ET irrigation resulted in a reduction in leaf number, leaf area, and plant dry weight in great bougainvillea (*Bougainvillea spectabilis* Willd.) ‘Aurantiaca’. In contrast, *B. ×buttiana* Holtum & Standl. ‘Rosenka’, with better water transport due to a wider stem diameter and thicker xylem tissues, did not show significant reductions in leaf growth and dry weight under the 25% ET irrigation (Cirillo et al. 2017). Crimson bottlebrush [*Melaleuca citrina* (Curtis) Dum.Cours.] exhibited a reduction in whole plant dry weight, leaf number, leaf area and plant height under the 40% field capacity (FC) irrigation treatment compared to the 100% FC irrigation treatment, which corresponds to approximately 54% volumetric water content (Álvarez et al. 2011). Additionally, there was an increase in the root-to-shoot ratio, indicating a shift in photo-assimilate allocation in response to water availability (Cirillo et al. 2017). A 40% water holding capacity (WHC) treatment reduced the dry weight, leaf area, plant height, Fv/Fm, Pn, and g<sub>s</sub> of mastic tree (*Pistacia lentiscus* L.) when compared to the 100% WHC treatment, but the root-to-shoot ratio was not significantly affected (Álvarez et al. 2018).

Excessive moisture or waterlogging can have detrimental effects on woody plants, leading to a reduction in leaf number, inhibition of leaf formation and expansion, and the promotion of early chlorophyll degradation, leaf yellowing, and abscission. Notably, waterlogging tends to have a more significant impact on the root system than on shoot growth in woody plants (Kozłowski 1997). Assessing photosynthetic parameters can be valuable in gauging the waterlogging tolerance of woody plants, serving as indicative markers of their ability to cope with waterlogged conditions. The waterlogging treatment resulted in a reduction in leaf dry weight, Pn, and g<sub>s</sub> of silver buttonwood (*Conocarpus erectus* L.), mahogany [*Swietenia mahagoni* (L.) Jacq.], and Surinam cherry (*Eugenia uniflora* L.). However, pond apple (*Annona glabra* L.) was less affected by waterlogging, indicating its suitability for nurseries in easily flooded areas (Martin et al. 2010). In distylium [*Distylium chinense* (Franch. ex Hemsl.) Diels], waterlogging causes mild wilting and yellowing of old leaves, accompanied by a decrease in the number of new leaves. Both Pn and g<sub>s</sub> were significantly reduced in the early stages of waterlogging, indicating that stomatal factor was the major cause of the lowered photosynthesis (Liu et al. 2014). As the duration of waterlogging was extended, the intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) gradually increased, and Fv/Fm decreased. These changes indicate damage to the photosystem, reduced electron transfer, and lower energy conversion efficiency, and non-stomatal factors becoming the major cause of lowered photosynthesis in later stages of waterlogging (Liu et al. 2014). Waterlogging had adverse effects on yellow trumpet tree [*Handroanthus chrysotrichus* (Mart. ex DC.) Mattos], leading to root tip necrosis, reduced chlorophyll content, and a decrease in plant dry weight. In the early stages of waterlogging, both Pn and g<sub>s</sub> decreased (Bispo and Vieira 2022). After 40 days of waterlogging, there was an increase in C<sub>i</sub> and the hindrance of

electron transfer in the photosystem of yellow trumpet tree (Bispo and Vieira 2022).

The capacitance soil moisture sensor, such as the WET sensor, employs frequency domain reflectometry to measure volumetric water content (VWC) in the soil or medium by assessing dielectric permittivity and bulk electrical conductivity. This instrument provides several advantages, including low regular maintenance, easy calibration, and low susceptibility to reading errors (Burnett and van Iersel 2008). The objective of this study was to investigate the effects of medium VWC on the growth and photosynthesis of *R. hainanensis* and *R. sinica*.

## Materials and Methods

**Plants and irrigation treatments.** Young seedlings of *Radermachera hainanensis* and *R. sinica*, each with six to eight pairs of leaves, were transplanted into 1-L (0.26 gal) plastic pots containing a mixture of 3 peatmoss (pH balanced peat moss, Klasmann-Deilmann GmbH, Geeste, Germany): 1 perlite (No.2, Nanhai Vermiculite Industrial Co., New Taipei City, Taiwan): 1 vermiculite (No.2, Nanhai Vermiculite Industrial Co., New Taipei City, Taiwan) by volume and supplemented with 6 g (0.21 oz) of 13N-4.8P-10.8K slow-release-fertilizer containing micronutrients (S101 13-11-12-2TE, JCAM-AGRI Co., Tokyo, Japan) per pot. Plants were transferred into a greenhouse at mean 29.7 C (85.5 F) and 1750 μmol·m<sup>-2</sup>·s<sup>-1</sup> maximum noon photosynthetic photon flux (PPF) (162.6 ft-c) at plant height to receive their irrigation treatments.

There were four irrigation treatments given during the 103-day experimental period, as follows:

1. Dry condition: Each plant was irrigated with 100 mL (3.4 oz) of reverse osmosis (RO) water whenever the VWC dropped below 20%.
2. Dry/wet cycle: A dry/wet cycle was established by thoroughly irrigating with RO water until full capacity whenever the VWC was lower than 20%.
3. Even moisture: Each plant was irrigated with 300 mL (10.1 oz) of RO water whenever the VWC fell below 40%.
4. Waterlogging: Potted plants were placed into plastic buckets filled with RO water up to 10 cm (3.9 in) above the bottom of the pots.

VWCs at 10 cm (3.9 in) below the medium surface were measured during 0900-1200 HR with WET sensor (Type HH2; Delta-T Devices, Cambridge, UK) before irrigation. There were ten plants of each species for each irrigation treatment.

**Measurements of parameters of photosystem II and photosynthesis.** At 92 d after treatments began, the recently fully expanded leaves from each plant were sampled to measure chlorophyll fluorescence parameters using a portable chlorophyll fluorometer Mini-Pam (Heinz Walz GmbH, Effeltrich, Germany). The fluorescence ratio Fv/Fm, non-photochemical quenching (qN), and actual photochemical quantum yield (ΦPSII) were measured.

At 102 d after treatments being initiated, photosynthetic parameters were assessed using a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA). Air was

pumped through a desiccant (Drierites, 97% CaSO<sub>4</sub> + 3% CaCl<sub>2</sub>, W.A. Hammond Drierite Co., Xenia, OH, USA) and LI-COR soda lime (LI-COR, Lincoln, NE, USA) to eliminate excess water vapor and CO<sub>2</sub>. Light intensity within leaf chamber was set at 1000 μmol·m<sup>-2</sup>·s<sup>-1</sup> PPF (92.9 ft-c) and a reference CO<sub>2</sub> concentration of 400 μmol·mol<sup>-1</sup> was provided. The air flow rate was set at 600 μmol·s<sup>-1</sup>, and the measurement area was set at 3 cm<sup>2</sup> (0.465 in<sup>2</sup>). Temperature at the leaf surface was maintained at an average of 27.5 C (81.5 F). This allowed for the measurement of the P<sub>n</sub>, g<sub>s</sub>, transpiration rate (E), and C<sub>i</sub> of the most recently fully expanded leaves.

**Measurements of growth.** At 103 d after treatments began, plant height, stem diameter, and total leaflet number were measured. The relative chlorophyll content of the most recently fully expanded leaf was also measured in situ with a chlorophyll meter (SPAD-502, Minolta Camera Co., Tokyo, Japan). Leaf area of the most recently fully expanded leaf was calculated using Image J. Number of dropped leaflets during the experimental duration was counted and recorded. Plants were divided into above-ground (shoot) and below-ground (roots) parts, oven-dried at 70 C (158 F) until constant, and recorded for dry weights. The root-to-shoot ratio was calculated as root dry weight divided by shoot dry weight. Relative dry weight was calculated as the ratio of shoot and root dry weights in plants under the waterlogging, dry and dry/wet conditions to those under the even moisture condition, respectively.

This experiment was arranged in a completely randomized design. Comparison between different treatment means was made by least significant difference (LSD) at *P* < 0.05 using CoStat 6.4 (CoHort Software, Monterey, CA, USA).

## Results and Discussion

**Irrigation treatments.** After three days and thereafter, the VWC for the waterlogging treatment remained approximately 70% throughout the experiment (shown as 70% VWC). Measurements of the other medium VWC indicated that it took 14 days to reach designated VWC. The VWC for the dry treatment throughout the experiment ranged from 16% to 28% (Fig. 1), with a mean of 20% VWC (hereafter shown as 20% VWC). In the dry/wet cycle treatment, the VWC during dry and wet periods was 20% and 60%, respectively (shown as 20%/60% VWC), with a mean of 40% VWC. The VWC for the even moisture treatment ranged from 33% to 50%, with a mean of 40% VWC (shown as 40% VWC).

**Growth responses.** The two *Radermachera* species subjected to the 20% VWC treatment exhibited the lowest leaf area and leaflet number (Fig. 2A and E; Table 1). Similar reductions in leaf growth due to drought stress have been reported for woody ornamentals, including great bougainvillea ‘Lindleyana’ (Cirillo et al. 2017), lantana and Chinese privet (Toscano et al. 2018), and crimson bottlebrush (Álvarez et al. 2011). Drought suppresses turgor pressure and cell expansion, which are crucial for leaf area development. Water stress may alter the functioning of growth regulators and cell division, leading to a reduction in leaf

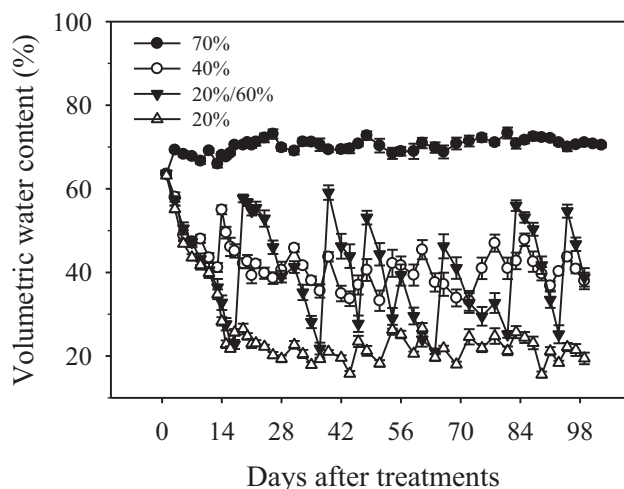


Fig. 1. Changes in volumetric water content (VWC) over time for each irrigation treatment (n = 10, means ± SE).

number (Hsiao 1973, Taiz and Zeiger 2006). The decreased leaf number and leaf area resulted in diminished photosynthetic capacities and assimilates, possibly explaining why these two *Radermachera* species subjected to the 20% VWC treatment were the shortest with the smallest stem diameter (Fig. 2A and E; Table 1).

In comparison to plants with the 20% VWC, the 20%/60% VWC treatment resulted in increased stem diameter and leaf area for both species (Fig. 2B and F; Table 1). This agrees with the concept that turgor-dependent attributes, such as leaf area, are the most sensitive to water deficit (Taiz and Zeiger 2006, Toscano et al. 2018). The 20%/60% VWC treatment resulted in an increase in leaflet number and a reduction in leaf drop number in *R. sinica* but not in *R. hainanensis* as compared with the 20% VWC treatment. The two *Radermachera* species exposed to 40% VWC exhibited the best growth performance, with the maximum stem diameter, leaf area, and root dry weight (Fig. 2C and G; Table 1). This aligns with the high water demands for China Doll, as reported by Poole and Conover (1992), whereas *R. hainanensis* is more susceptible to prolonged drought stress than *R. sinica*. The two *Radermachera* species subjected to the 70% VWC exhibited smaller stem diameters and lower leaf SPAD-502 values than those exposed to 40% VWC (Fig. 2D and H; Table 1). Flooding can affect the structural integrity of chloroplasts and lead to chlorophyll degradation (Kuai et al. 2014, Ren et al. 2016), resulting in decreased chlorophyll content, as reported in woody ornamental plants such as distylium (Liu et al. 2014) and yellow trumpet tree (Bispo and Vieira 2022).

In the case of *R. hainanensis*, the 20% VWC treatment resulted in the lowest shoot and root dry weights (Fig. 3; Table 2). Dry weight and relative dry weight did not differ between plants treated with the 20%/60% VWC and those with the 40% VWC treatments. Plants of *R. hainanensis* treated with the 20%/60% VWC exhibited higher root dry weight than those subjected to the 20% VWC treatment, but root dry weight was still lower than in the 40% VWC treatment. The root-to-shoot ratio was highest in *R. sinica* with the 20% VWC treatment but did not differ among the VWC

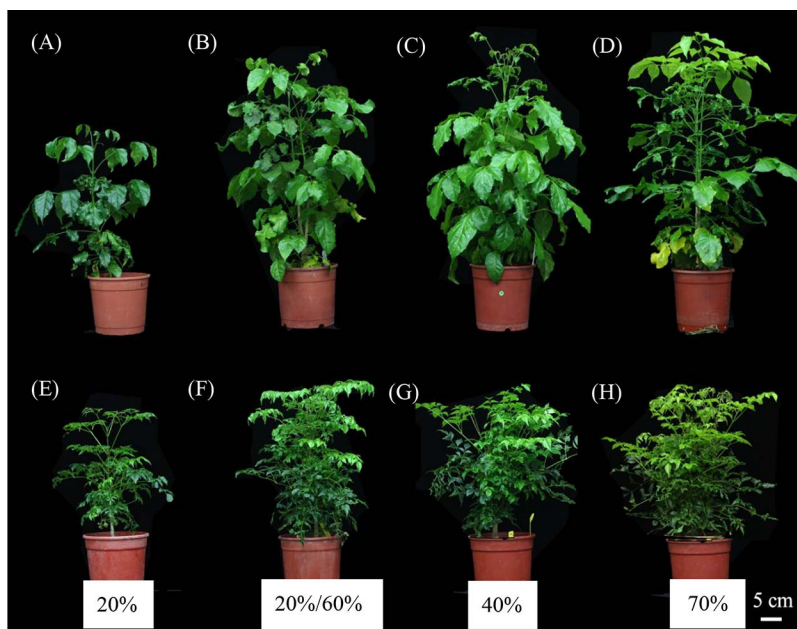


Fig. 2. Plant appearance of *Radermachera hainanensis* (A-D) and *R. sinica* (E-H) after various irrigation treatments.

treatments for *R. hainanensis*. These results align with previous reports indicating that shoots and roots respond differently to drought stress (Álvarez et al. 2009, Mugnai et al. 2005). The root-to-shoot biomass ratio is influenced by a functional balance between water uptake by the roots and photosynthesis by the shoots. The increased root-to-shoot ratio observed in *R. sinica* under drought conditions can be considered as a morphological adaptation to water stress to reduce the evaporative surface area and to induce a lower water consumption (De Herralde et al. 1998, Taiz and Zeiger 2006). Similar changes in the root-to-shoot adaptive mechanism to drought have been reported for lantana and Chinese privet (Toscano et al. 2018). *Radermachera hainanensis* appears to necessitate more irrigation for the expansion of larger leaflets and greater biomass, and it lacks a root-to-shoot adaptive mechanism to water-deficit when grown in pots compared to *R. sinica*. The 70% VWC treatment did not alter shoot dry weight but led to lower root dry weight compared to the 40% VWC for *R. hainanensis* (Fig. 3; Table 2). This aligns with previous reports demonstrating that root growth is more significantly reduced than shoot

growth in woody plants under flooding conditions (Kozłowski 1997).

*Responses of chlorophyll fluorescence and photosynthetic parameters.* Both *Radermachera* species treated with 20% VWC exhibited decreased Fv/Fm values (Table 3), falling below the typical range of 0.75–0.85 for non-stressed plants (Krause and Weis 1991). The Fv/Fm value was successfully utilized to monitor the adaptability to the drought stress. The Fv/Fm values are maintained between 0.75 and 0.8 for drought-tolerant woody plants (Álvarez et al. 2011, Percival and Sheriffs 2002). The 20% VWC treatment increased qN and decreased ΦPSII in both *Radermachera* species (Table 3), indicating that drought led to the excess absorbed light energy being dissipated thermally and a decreased efficiency of electron transport, as reported for many drought-stressed plants (Bukhov and Carpentier 2004). The 70% VWC treatment resulted in a decreased Fv/Fm value in *R. hainanensis* but did not alter the Fv/Fm in *R. sinica* (Table 3). We observed that under waterlogging conditions, *R. sinica* developed more adventitious roots, which are

Table 1. Effects of volumetric water content (VWC) treatments on plant height, stem diameter, and leaf growth of *Radermachera hainanensis* and *R. sinica* after treatments for 103 days.

VWC (%)	Plant height (cm)	Stem diameter (mm)	Total leaflet number	SPAD-502 value	Leaf area (cm <sup>2</sup> )	Number of leaflets dropped
<i>R. hainanensis</i>						
20	22.4 b <sup>z</sup>	9.4 c	46.2 b	41.7 a	32.8 b	10.0 a
20/60	29.3 b	12.5 b	61.5 ab	36.5 ab	74.1 a	9.3 a
40	40.0 a	16.0 a	69.9 a	36.8 ab	87.5 a	3.9 b
70	45.0 a	14.0 b	65.3 a	32.7 b	81.9 a	5.9 b
<i>R. sinica</i>						
20	26.3 b	9.2 c	58.5 b	39.2 a	18.6 b	14.9 a
20/60	29.1 ab	10.9 b	134.9 a	36.3 ab	63.1 a	11.5 b
40	33.9 a	12.9 a	148.9 a	36.7 ab	75.8 a	10.1 b
70	32.5 a	10.5 b	156.3 a	32.9 b	72.4 a	11.4 b

<sup>z</sup>Mean separation within columns and species according to the least significant difference at  $P < 0.05$  ( $n = 10$ ).

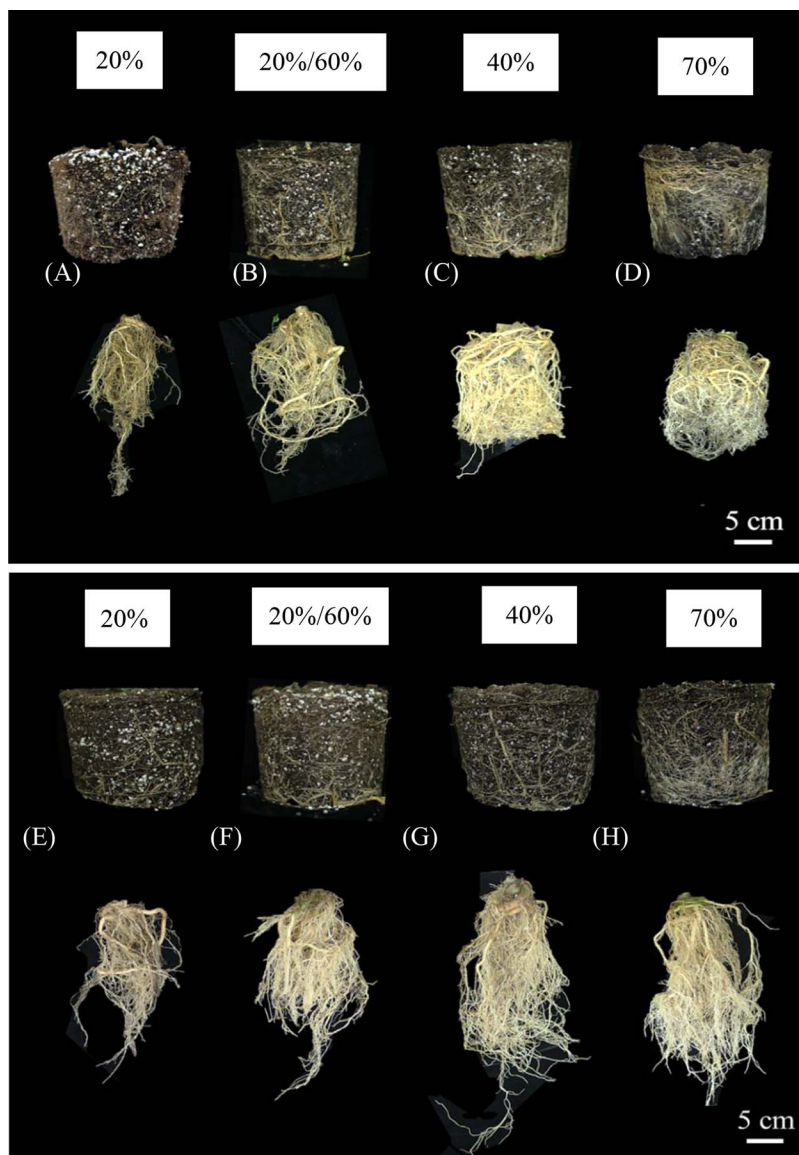


Fig. 3. Root appearance of *Radermachera hainanensis* (A-D) and *R. sinica* (E-H) after various irrigation treatments.

considered morphological adaptations for flood-tolerant woody plants (Kozłowski 1997).

Both *Radermachera* species subjected to the 20% VWC exhibited the lowest  $P_n$ ,  $g_s$ , and E, indicating a stomatal

limitation. The reduction in  $P_n$ ,  $g_s$ , and E with the 20% VWC was more pronounced in *R. hainanensis* (Table 4). The decrease in  $P_n$  through stomatal closure or reduced  $g_s$  has been well documented for water-deficient plants

Table 2. Effects of volumetric water content (VWC) treatments on plant weight, root to shoot ratio, and relative shoot, root dry weight compared to the 40% VWC treatment in *Radermachera hainanensis* and *R. sinica* after treatments for 103 days.

VWC (%)	Dry weight (g)		Root to shoot ratio	Relative dry weight (%)	
	Shoot	Root		Shoot	Root
	<i>R. hainanensis</i>				
20	11.8 b <sup>2</sup>	6.2 c	0.52 a	38.9 b	29.9 c
20/60	22.8 ab	12.1 b	0.56 a	78.1 ab	58.1 b
40	30.4 a	20.8 a	0.68 a	100.0 a	100.0 a
70	32.9 a	14.9 b	0.61 a	108.1 a	71.6 b
	<i>R. sinica</i>				
20	8.3 b	8.9 a	1.21 a	43.7 b	88.5 a
20/60	14.1 a	10.1 a	0.71 b	74.4 ab	99.6 a
40	19.0 a	10.1 a	0.54 b	100.0 a	100.0 a
70	19.0 a	7.8 a	0.48 b	100.2 a	77.2 a

<sup>2</sup>Mean separation within columns and species according to the least significant difference at  $P < 0.05$  ( $n = 5$ ).

**Table 3. Effects of volumetric water content (VWC) treatments on maximum efficiency of PSII (Fv/Fm), non-photochemical quenching (qN), and actual efficiency of PSII (ΦPSII) in *Radermachera hainanensis* and *R. sinica* after treatments for 92 days.**

VWC (%)	Fv/Fm	qN	ΦPSII
		<i>R. hainanensis</i>	
20	0.72 b <sup>z</sup>	0.06 a	0.62 b
20/60	0.77 a	0.02 b	0.68 a
40	0.77 a	0.02 b	0.68 a
70	0.73 b	0.03 b	0.65 ab
		<i>R. sinica</i>	
20	0.72 b	0.06 a	0.58 c
20/60	0.77 a	0.03 b	0.64 bc
40	0.78 a	0.03 b	0.72 a
70	0.77 a	0.03 b	0.68 ab

<sup>z</sup>Mean separation within columns and species according to the least significant difference at  $P < 0.05$  ( $n = 5$ ).

(Álvarez et al. 2018, Hsiao 1973, Taiz and Zeiger 2006). *Radermachera sinica* under the 20% VWC exhibited the highest  $C_i$  (Table 4), suggesting also the involvement of non-stomatal limitations. Both *Radermachera* species exhibited higher  $Pn$  with the 20%/60% VWC than with the 20% VWC, consistent with the growth response as shown in Tables 1 and 2. The  $g_s$  was lower with the 20%/60% VWC than the 40% VWC in *R. hainanensis*. In contrast, *R. sinica* under the 20%/60% VWC exhibited a reduced  $C_i$ , and the  $g_s$  did not differ between the 20%/60% VWC and 40% VWC treatments (Table 4), suggesting that the 20%/60% VWC treatment increased  $Pn$  through the reduction of both stomatal and non-stomatal limitations. *Radermachera hainanensis* exhibited lower  $Pn$  with the 70% VWC treatment compared to the 40% VWC treatment (Table 4). This might be attributed to a more substantial reduction in both root dry weight and Fv/Fm in *R. hainanensis* with waterlogging (Fig. 3; Tables 2 and 3), leading to decreased water and mineral element uptake (Ashraf and Arfan 2005), resulting in decreased photosynthesis and photoassimilate (Zhang et al. 2018). In contrast, *R. sinica* exposed to the 70% VWC treatment, although exhibited a slight increased  $C_i$ , maintained high  $Pn$ ,  $g_s$ , and E as those with the 40% VWC treatment (Table 4). Similar results have been reported in tropical woody plants from seasonally flooded areas (Herrera et al. 2008). China Doll grown under the 70% VWC treatment produced more adventitious roots (Fig. 3), which is considered as a morphological adaptation for flood-tolerant plants to survive waterlogging (Kozłowski 1997).

Both *Radermachera* species prefer an even moisture growing medium and are not tolerant to drought conditions, which reduced plant height, stem diameter, leaf area and decreased  $Pn$ ,  $g_s$ , Fv/Fm, and qN. China Doll showed a better recovery after post-drought irrigation (20%/60% VWC) and exhibited more adaptation to waterlogging than *R. hainanensis* (Tables 1 and 2). This information would provide valuable insights into the water management practices for the optimal growth of these tropical plants. It is suggested that these two *Radermachera* species, characterized by various pinnate-compound leaves and varying leaflet sizes, could serve as a promising model for studying the

**Table 4. Effects of volumetric water content (VWC) treatments on net photosynthetic rate ( $Pn$ ,  $\mu\text{mol CO}_2\text{-m}^{-2}\text{-s}^{-1}$ ), stomatal conductance ( $g_s$ ,  $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), transpiration rate (E,  $\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and intercellular  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol}\cdot\text{mol}^{-1}$ ) of the recently fully expanded leaves in *Radermachera hainanensis* and *R. sinica* after treatments for 102 days.**

VWC (%)	$Pn$	$g_s$	E	$C_i$
		<i>R. hainanensis</i>		
20	1.7 c <sup>z</sup>	0.033 b	0.63 b	246 c
20/60	4.1 b	0.040 b	0.93 b	252 bc
40	6.8 a	0.093 a	1.61 a	265 ab
70	4.3 b	0.073 a	1.41 a	278 a
		<i>R. sinica</i>		
20	2.8 c	0.048 c	0.69 c	297 a
20/60	4.6 b	0.056 bc	0.92 b	274 b
40	5.6 a	0.072 ab	1.28 a	256 c
70	5.2 a	0.077 a	1.34 a	273 b

<sup>z</sup>Mean separation within columns and species according to the least significant difference at  $P < 0.05$  ( $n = 5$ ).

fundamental aspects of hydraulic architecture, including water relationships, gas exchange, and their distribution across different habitats.

## Literature Cited

- Álvarez, S., P. Rodríguez, F. Broetto, and M.J. Sánchez-Blanco. 2018. 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. *Agric. Water Manag.* 202:253-262. doi: 10.1016/j.agwat.2018.01.006.
- Álvarez, S., A. Navarro, E. Nicolás, and M.J. Sánchez-Blanco. 2011. Transpiration, photosynthetic responses, tissue water relations and dry mass partitioning in *Callistemon* plants during drought conditions. *Sci. Hortic.* 129:306-312. doi: 10.1016/j.scienta.2011.03.031.
- Álvarez, S., A. Navarro, S. Bañón, and M.J. Sánchez-Blanco. 2009. Regulated deficit irrigation in potted *Dianthus* plants: Effects of severe and moderate water stress on growth and physiological responses. *Sci. Hortic.* 122:579-585. doi: 10.1016/j.scienta.2009.06.030.
- Ashraf, M. and M. Arfan. 2005. Gas exchange characteristics and water relations in two cultivars of *Hibiscus esculentus* under waterlogging. *Biol. Plant.* 49:459-462. doi: 10.1007/s10535-005-0029-2.
- Bispo, T.M. and F.A. Vieira. 2022. Assimilatory deficit and energy regulation in young *Handroanthus chrysotrichus* plants under flooding stress. *J. Plant Res.* 135:323-336. doi: 10.1007/s10265-022-01370-3.
- Bukhov, N.G. and R. Carpentier. 2004. Effects of water stress on the photosynthetic efficiency of plants. p. 623-635 In: G.C. Papageorgiou and Govindjee (Eds.). *Chlorophyll a Fluorescence*. Springer, Dordrecht, The Netherlands. doi: 10.1007/978-1-4020-3218-9\_24.
- Burnett, S.E. and M.W. van Iersel. 2008. Morphology and irrigation efficiency of *Gaura lindheimeri* grown with capacitance sensor-controlled irrigation. *HortSci.* 43:1555-1560. doi: 10.21273/HORTSCI.43.5.1555.
- Cirillo, C., Y. Roupael, R. Caputo, and G. Raimondi. 2017. The influence of deficit irrigation on growth, ornamental quality, and water use efficiency of three potted *Bougainvillea* genotypes grown in two shapes. *HortSci.* 49:1284-1291. doi: 10.21273/HORTSCI.49.10.1284.
- De Herralde, F., C. Biel, R. Savé, M.A. Morales, A. Torrecillas, J.J. Alarcón, and M.J. Sánchez-Blanco. 1998. Effect of water and salt stresses on the growth, gas exchange and water relations in *Argyranthemum coronopifolium* plants. *Plant Sci.* 139:9-17. doi: 10.1016/S0168-9452(98)00174-5.
- Dunlap, J.R., Y.T. Wang, and A. Skaria. 1994. Abscisic acid- and ethylene-induced defoliation of *Radermachera sinica* L. *Plant Growth Regul.* 14:243-248. doi: 10.1007/BF00024799.

- Griffith, L.P. 2006. Tropical foliage plants: a grower's guide. Ball Pub., Batavia, IL. 357 p.
- Herrera, A., W. Tezara, O. Marín, and E. Rengifo. 2008. Stomatal and non-stomatal limitations of photosynthesis in trees of a tropical seasonally flooded forest. *Physiol. Plant.* 134:41-48. doi: 10.1111/j.1399-3054.2008.01099.x.
- Hsiao, T.C. 1973. Plant responses to water stress. *Annu. Rev. Plant Physiol.* 24:519-570. doi: 10.1146/annurev.pp.24.060173.002511.
- Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. *Tree Physiol.* 17:490-449. doi: 10.1093/treephys/17.7.490.
- Krause, G.H. and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis: The basics. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 42:313-349. doi: 10.1146/annurev.pp.42.060191.001525.
- Kuai, J., Z. Liu, Y. Wang, Y. Meng, B. Chen, W. Zhao, Z. Zhou, and D.M. Oosterhuis. 2014. Waterlogging during flowering and boll forming stages affects sucrose metabolism in the leaves subtending the cotton boll and its relationship with boll weight. *Plant Sci.* 223:79-98. doi: 10.1016/j.plantsci.2014.03.010.
- Liu, Z., R. Cheng, W. Xiao, Q. Guo, and N. Wang. 2014. Effect of off-season flooding on growth, photosynthesis, carbohydrate partitioning, and nutrient uptake in *Distylium chinense*. *PLoS One* 9:e107636. doi: 10.1371/journal.pone.0107636.
- Martin, C.G., B. Schaffer, and C. Mannion. 2010. Effects of flooding on physiology and growth of four woody ornamental species in marl soil of south Florida. *J. Environ. Hort.* 28:159-165. doi: 10.24266/0738-2898-28.3.159.
- Mugnai, S., G. Serra, F. Malorgio, and P. Vernieri. 2005. Response of some ornamental shrubs to different soil water conditions. *Adv. Hortic. Sci.* 19:1-7. doi: 10.1400/14367.
- Pan, J., R. Sharif, X. Xu, and X. Chen. 2021. Mechanisms of waterlogging tolerance in plants: Research progress and prospects. *Front. Plant Sci.* 11:627331. doi: 10.3389/fpls.2020.627331.
- Percival, G.C. and C.N. Sheriffs. 2002. Identification of drought-tolerant woody perennials using chlorophyll fluorescence. *J. Arboric.* 28:215-223. doi: 10.48044/jauf.2002.032.
- Poole, R.T. and C.A. Conover. 1992. Paclobutrazol and indoor light intensity influence water use of some foliage plants. *Proc. Fla. State. Hortic. Soc.* 105:178-180.
- Ren, B., J. Zhang, S. Dong, P. Liu, and B. Zhao. 2016. Effects of waterlogging on leaf mesophyll cell ultrastructure and photosynthetic characteristics of summer maize. *PLoS One* 11:e0161424. doi: 10.1371/journal.pone.0161424.
- Taiz, L. and E. Zeiger. 2006. *Plant physiology*. 4th ed. Sinauer Associates Inc., Sunderland, England, U.K. 700 p.
- Thomas, M.B., M.I. Spurway, and B.A.J. Richards. 1995. Nutrition of container-grown *Radermachera sinica* Hemsl. *N. Z. J. Crop Hortic. Sci.* 23:461-465. doi: 10.1080/01140671.1995.9513924.
- Toscano, S., A. Ferrante, A. Tribulato, and D. Romano. 2018. Leaf physiological and anatomical responses of *Lantana* and *Ligustrum* species under different water availability. *Plant Physiol. Biochem.* 127:380-392. doi: 10.1016/j.plaphy.2018.04.008.
- Zhang, H., P. Feng, W. Yang, X. Sui, X. Li, W. Li, R. Zhang, S. Gu, and N. Xu. 2018. Effects of flooding stress on the photosynthetic apparatus of leaves of two *Physocarpus* cultivars. *J. For. Res.* 29:1049-1059. doi: 10.1007/s11676-017-0496-2.