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Plant Physiology/ Original Article

Drought/rewatering cycles on the vegetative growth of citrus seedlings

Abstract – The objective of this work was to evaluate the effect of three dehydration/rehydration cycles on the vegetative growth and shoot dry matter of citrus seedlings, as well as seedling acclimatization to this environmental stress. The five following water regimes were evaluated: WR1 (control), WR2, and WR3, with plants kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; and WR4 and WR5, with plants kept at 75, 100, and 75% and 50, 100, and 50% of pot capacity during the first, second, and third cycles, respectively. Relative water content, plant height, length and diameter of the main and secondary branches, angle of leaf insertion in the branch, specific leaf area, leaf chlorophyll content, and dry matter were evaluated. Rehydration after a cycle with 50% of pot capacity did not improve plant growth or dry matter accumulation in relation to the well-hydrated plants of the control. However, after a cycle with 75% of pot capacity, rehydration restores water content, the diameter of the secondary branches, and the angle of leaf insertion. The exposure to successive events of dehydration/rehydration makes the citrus seedlings more resistant to future exposures to water stress.

Index terms: *Citrus reticulata*, angle of leaf insertion, leaf area, relative water content, seedling growth, water regimes.

Ciclos de seca/reidratação no crescimento vegetativo de mudas de citros

Resumo – O objetivo deste trabalho foi avaliar o efeito de três ciclos consecutivos de desidratação/reidratação no crescimento vegetativo e na matéria seca de mudas de citros, bem como a aclimatação dessas mudas a esse estresse ambiental. Foram avaliados os seguintes cinco regimes hídricos: WR1 (controle), WR2 e WR3, com plantas mantidas em 100, 75 e 50% da capacidade de vaso durante os três ciclos, respectivamente; e WR4 e WR5, com plantas mantidas em 75, 100 e 75% e 50, 100 e 50% da capacidade de vaso durante o primeiro, o segundo e o terceiro ciclo, respectivamente. Foram avaliados teor relativo de água, altura da planta, comprimento e diâmetro dos ramos principal e secundário, ângulo de inserção da folha no ramo, área foliar específica, teor de clorofila foliar e matéria seca. A reidratação após um ciclo com 50% da capacidade do vaso não aumentou o crescimento nem o acúmulo de matéria seca das plantas, em comparação às plantas bem hidratadas do controle. Porém, após um ciclo com 75% da capacidade do vaso, a reidratação repôs o teor de água, o diâmetro dos ramos secundários e o ângulo de inserção das folhas. A exposição a sucessivos eventos de desidratação/reidratação torna as mudas de citros mais resistentes a futuras exposições ao estresse hídrico.

Termos para indexação: *Citrus reticulata*, ângulo de inserção foliar, área foliar, teor relativo de água, crescimento de mudas, regimes hídricos.

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Introduction

Recent studies have shown that, over time, plants exposed to successive stress events are able to respond more quickly and vigorously to the stressor by retrieving previously stored information on the biochemical and/or epigenetic changes that occur after the first exposure, allowing of different physiological responses (Dong et al., 2019). Therefore, a previous water deficit can be used to prepare plants for consecutive water deficit events (Fleta-Soriano & Munné-Bosch, 2016; Guedes et al., 2019), through adjustments under the same abiotic condition that can be effective in protecting the plant (Guedes et al., 2019; Wojtyla et al., 2020).

In citrus (*Citrus* spp.) trees, studies on water deficit events have been carried out with different purposes, to determine, for example: the differential response to drought and rehydration in the leaves and roots of different rootstocks (Gonçalves et al., 2016; Santos et al., 2017; Sousa et al., 2022); the influence of a recurrent water deficit on plant genetic, metabolic, and physiological processes (Neves et al., 2017, 2018); and the effect of dehydration/rehydration on fruit quality (Romero et al., 2021). The obtained results allow of concluding that plant exposure to controlled cycles of dehydration/rehydration is an essential tool to increase plant tolerance to water stress under field conditions and to reduce damage to fruit quality and yield. However, these researches mainly evaluated plants in the reproductive and not in the seedling stage, which is crucial for establishing a vigorous and productive crop.

The objective of this work was to evaluate the effect of three dehydration/rehydration cycles on the vegetative growth and shoot dry matter of citrus seedlings, as well as seedling acclimatization to this environmental stress.

Materials and Methods

The experiment was carried out during springtime under greenhouse conditions in the municipality of Lavras, in the south of the state of Minas Gerais, Brazil (21°13'40"S, 44°57'50"W, at 919 m above sea level.) According to Köppen’s classification (Alvares et al., 2013), the climate of the region is Cwa, with a cold and dry winter and a hot and humid summer, with an annual mean temperature of 19.3°C.

For the study, six-month-old plants of 'Ponkan' mandarin (*Citrus reticulata* Blanco) were grafted onto 'Rangpur' lime (*Citrus limonia* Osb.), obtained from Empresa de Pesquisa Agropecuária de Minas Gerais (Belo Horizonte, MG, Brazil). Individual plants were sown into 4.0 L pots (33.5 cm height x 14 cm diameter), containing a substrate with a 1:2 clay:sand ratio. The plants were fertilized six times during the experimental period to meet the nutritional requirements of the crop, according to Ribeiro et al. (1999). Greenhouse temperature and humidity were monitored hourly, three times, using the RHT10 thermo-hygrometer (Extech Instruments, Nashua, NH, USA).

After an acclimatization period of 30 days, in which the plants were kept under adequate irrigation and fertilization conditions, the imposition of the water regimes began. The plants were distributed into five water regimes over three consecutive dehydration/rehydration cycles, each lasting 8 days. Every 2 days, growth variables were evaluated, totaling four evaluation points per cycle. Before the beginning of each new cycle and dehydration phase, there was a space of 7 days to restore water condition, meaning that the experimental period lasted approximately 75 days, including the period of acclimatization and of water regime implementation during the three cycles.

The five evaluated water regimes were: WR1 (control), WR2, and WR3, in which the plants were kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; WR4, in which the plants were kept at 75% of pot capacity during the first cycle, rehydrated to 100% of pot capacity during the second cycle, and returned to 75% of pot capacity in the third cycle; and WR5, in which the plants were kept at 50% of pot capacity during the first cycle, rehydrated to 100% of pot capacity during the second cycle, and returned to 50% of pot capacity in the third cycle. Pot capacity was determined by rinsing the soil in four pot replicates until saturation, followed by leaching and drying until reaching a constant weight by subtracting the saturated and dry soil weight. Each water regime was composed of ten replicates with one plant per pot.

The growth variables evaluated during the experimental period were plant height, branch length, branch diameter, angle of leaf insertion, and leaf area, outlined in a triple factorial arrangement. The first, second, and third factors were, respectively: three dehydration/rehydration cycles; four evaluation points within each cycle, specifically on the second, fourth, sixth, and eighth day of each cycle; and the five water regimes, i.e., WR1, WR2, WR3, WR4, and WR5. At the end of the experimental period, relative water content, specific leaf area, leaf chlorophyll content, and leaf and branch dry matter were evaluated, with only one factor (water regimes).

To assess the leaf water status for each water regime, the relative water content (RWC) was determined at the end of the three dehydration/rehydration cycles (Neves et al., 2018). For this, the most recent, sun-exposed, and completely expanded leaves were harvested at 9 a.m. Five disks, each with a 1.5 cm diameter, were detached and weighed to obtain fresh weight (FW). Afterwards, the disks were placed in Petri dishes containing 10 mL distilled water and, then, in a refrigerator for 24 hours to determine turgid weight (TW), being, subsequently, oven dried, at 70°C, for 72 hours in order to estimate dry weight (DW). The RWC was calculated by [(FW - DW)/(TW - DW)] × 100. The same disks were used to obtain specific leaf area (SLA), expressed in cm^2 g^{-1} dry mass, through the equation SLA = $(\pi R^2)/(6 \times DW)$, where R is the radius of the disk. Leaf chlorophyll content was measured in five randomly selected fully-expanded leaves per plant using the SPAD 502 Plus portable chlorophyll meter (Spectrum Technologies, Inc., Aurora, IL, USA).

Plant height was measured with a meter stick from the bottom of the plant, where it touched the soil, to the top, where the youngest leaf was located. For each plant, the two branches with a substantial length and thickness were identified, classified according to their dimensions as main or secondary branch. The length (cm) and diameter (mm) of these branches were measured, as follows: from the branch insertion in the plant to the insertion of the younger leaves; and in the middle third of the branch, which was previously identified and marked, using a digital caliper. Additionally, the angle of leaf insertion (ALI) in the branch was determined using a protractor to measure the angle between the leaf stalk and central rib and the branch; for this, five leaves per replicate were randomly selected from different positions in the canopy. At the end of the experimental period, the plants were separated into leaves and branches and oven dried, at 70°C, until reaching a constant weight, in order to determine leaf and branch dry matter (g).

The total leaf area of the canopy was estimated for the five replicates per treatment. For this, in a photographic studio, a photo was taken downwards using the K430TV camera (LG Electronics Inc., Seoul, South Korea) in the same position and same period of the day, from 7 to 9 a.m. The used software was the Easy Leaf Area, developed by researchers at University of California (Davis, CA, USA), as described by Easlon & Bloom (2014).

Statistical analyses were conducted using the RStudio statistical software, version 2023.06.0 (Posit, Boston, MA, USA). Normality was checked by Shapiro-Wilk's test. To establish the significance of the effects of all factors (α=0.05), data were analyzed through the one-way analysis of variance. Means were separated by the least significant difference test (α=0.05). All variables were correlated with RWC using Pearson's statistical correlation analysis, considering significant correlations with at least $p<0.10$.

Results and Discussion

The leaf water status evaluated through the RWC variable at the end of the three dehydration/rehydration cycles was significantly influenced by the water regime ($F_{4.45}$ = 7.04, $p<0.001$). The plants grown in the WR3 and WR5 treatments, with at least two cycles with irrigation at 50% of daily evapotranspiration (pot capacity), showed a reduction of 15.44 and 18.94% in RWC in comparison with the control, meaning that, in WR5, rehydration did not allow of reaching the water status of WR1 (Figure 1). However, in WR2 and WR4, when the plants were kept at 75% of daily evapotranspiration for, at least, some cycles, rehydration led to RWC values of well-hydrated plants.

In the literature, other authors also observed that the application of water stress reduced RWC and that the effect of rehydration varies depending on factors such as stress intensity and duration, as well as the development stage in which it was imposed (Jin et al., 2015; Bortolheiro & Silva, 2017; Dong et al., 2019). The intensity of the stress determines the degree in which rehydration can reverse the decrease in RWC or even the degree of compensation in which it is possible to improve the ability of the plant to recover after stress imposition (Bortolheiro & Silva, 2017; Dong et al., 2019). In the present study, after a dry cycle with at least 50% of field capacity, the plant did not recover the water status of a fully hydrated plant even after being rehydrated.

Regarding the growth variables, there was a significant effect of water regime on plant height ($F_{4,540}$

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= 20.55, p<0.001), main branch length ($F_{4,540}$ = 5.41, p<0.001), secondary branch length ($F_{4,540}$ = 18.81, p<0.001), and leaf area ($F_{4,540}$ = 3.41, p<0.01). However, there was no significant effect of the evaluated points or cycles. In addition, RWC was positively correlated with pH (r = 0.89, p=0.043) and main branch length (r = 0.91, p=0.032), with nonsignificant correlations with leaf area and secondary branch length. In WR3 and WR5, the reduced water availability decreased all growth variables in relation to the control treatment, with differences of up to 5.9 for pH, 1.36 cm for main branch length, 1.67 cm for secondary branch length, and 527 cm^2 for leaf area (Figure 2). Even after complete rehydration, the plants that remained, at least, in one cycle with 50% of daily evapotranspiration did not achieve the values of the fully hydrated plants in WR1. However, in WR4, rehydration with at least 75% of daily evapotranspiration allowed of plants to reach values similar to those of well-hydrated plants.

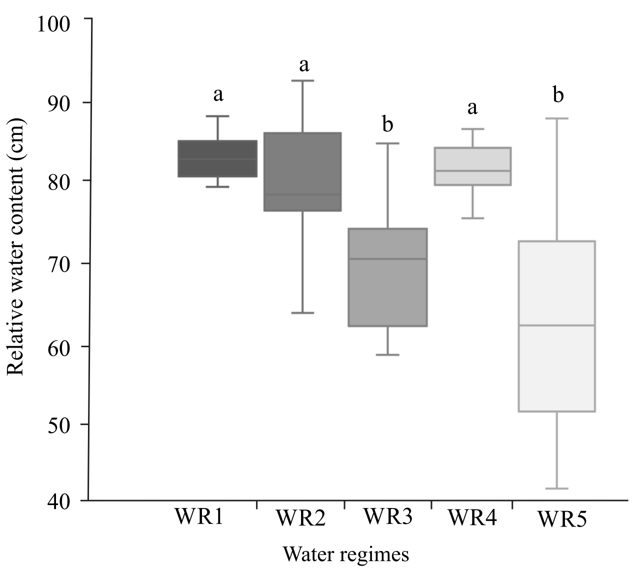

Figure 1. Relative water content of 'Ponkan' citrus (*Citrus reticulata*) plants grown under five water regimes (WR1–WR5) through three dehydration/rehydration cycles. WR1, WR2, and WR3, water regimes in which the plants were kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; and WR4 and WR5, water regimes in which the plants were kept at 75, 100, and 75% and 50, 100, and 50% of pot capacity during the first, second, and third cycles, respectively. Means (n = 10) followed by equal letters do not differ by the least significant difference test (LSD), at 5% probability. $LSD_{0.05}$ = 9.4054 on 45 degrees of freedom.

After rehydration, CO_2 assimilation and plant growth are usually re-established 1 to 2 days after the plants have been subjected to moderate water stress, but the time to full recovery may be longer after exposure to severe drought conditions (Sicher et al., 2012; Husen et al., 2014). This resumption of growth after rehydration was termed compensation by Dong et al. (2019), considered a possible plant self-defense against short-term, periodic, or unpredictable drought, in which growth is partially established to compensate for the losses caused by stress, sometimes even reducing differences in relation to the control group. In the present study, there were no significant differences between the evaluated cycles, which could indicate that, for the analyzed variables, the exposure to successive events of dehydration/rehydration does not reflect acclimatization to stress over time. However, considering the water regimes, WR4 showed the same values for secondary branch length as the control.

For main branch diameter, there was a significant effect of cycles ($F_{2,540}$ = 12.42, p<0.001) and of the interaction between cycles and evaluation points ($F_{6,540}$ = 3.61, p<0.01), but not of water regimes ($F_{4,540}$ = 1.38, ns). However, for secondary branch diameter, there was a significant influence of cycles ($F_{2,540}$ = 18.91, p<0.001), evaluation points ($F_{3,540}$ = 8.52, p<0.001), water regimes ($F_{4,540}$ = 7.73, p<0.001), and the interaction between cycles and evaluation points per cycle ($F_{6,540}$ = 12.26, p<0.001). Neither of the variables, however, showed significant correlations with RWC. On average, after three cycles of dehydration/rehydration, the diameter of the main branch increased up to 0.57 cm and that of the secondary branch up to 0.38 cm, in comparison with the diameters obtained in the first cycle (Figure 3). For the interaction between cycles and evaluation points, there was a trend of the diameter of the branches increasing between the first and fourth evaluation points and between the three cycles consecutively. Moreover, the plants that remained in, at least, one cycle with 50% of daily evapotranspiration (WR3 and WR5) showed the lowest values for secondary branch diameter even after rehydration.

In their research, Husen et al. (2014) compared plants that received regular irrigation (control) for 15 days to those subjected to water stress for the same amount of time, concluding that the latter treatment caused a 13% reduction in basal stem diameter; however, after 5 days of rehydration, the stressed plants showed a significant partial recovery of 33% of the diameter recorded after the 15 days of stress. Considering the main branch diameter in the first cycle as 100%, there was an increase of 10% in this variable in the second and third cycles, considering the average for all water regime treatments and that there was no significant difference for this factor. Regarding the diameter of the secondary branch, taking into account the water regime factor and considering WR1 as 100%, there was a decrease of 12% in WR2, 3% in WR3, 6% in WR4, and 5% in WR5. For the cycle factor, considering the first cycle as 100%, there was an increase of 10% in this variable in the second and third cycles. These results suggest that the exposure to successive events of dehydration/rehydration is an indicative of some acclimatization for branch diameter, which showed higher values than those of the control treatment in the second and third cycles.

The ALI was the only variable significantly influenced by all sources of variation and their interaction ($F_{24,540}$ = 1.53, p<0.05). The highest values of ALI in the branch occurred in WR3, in which the plants were kept for at least one cycle or the entire experimental period

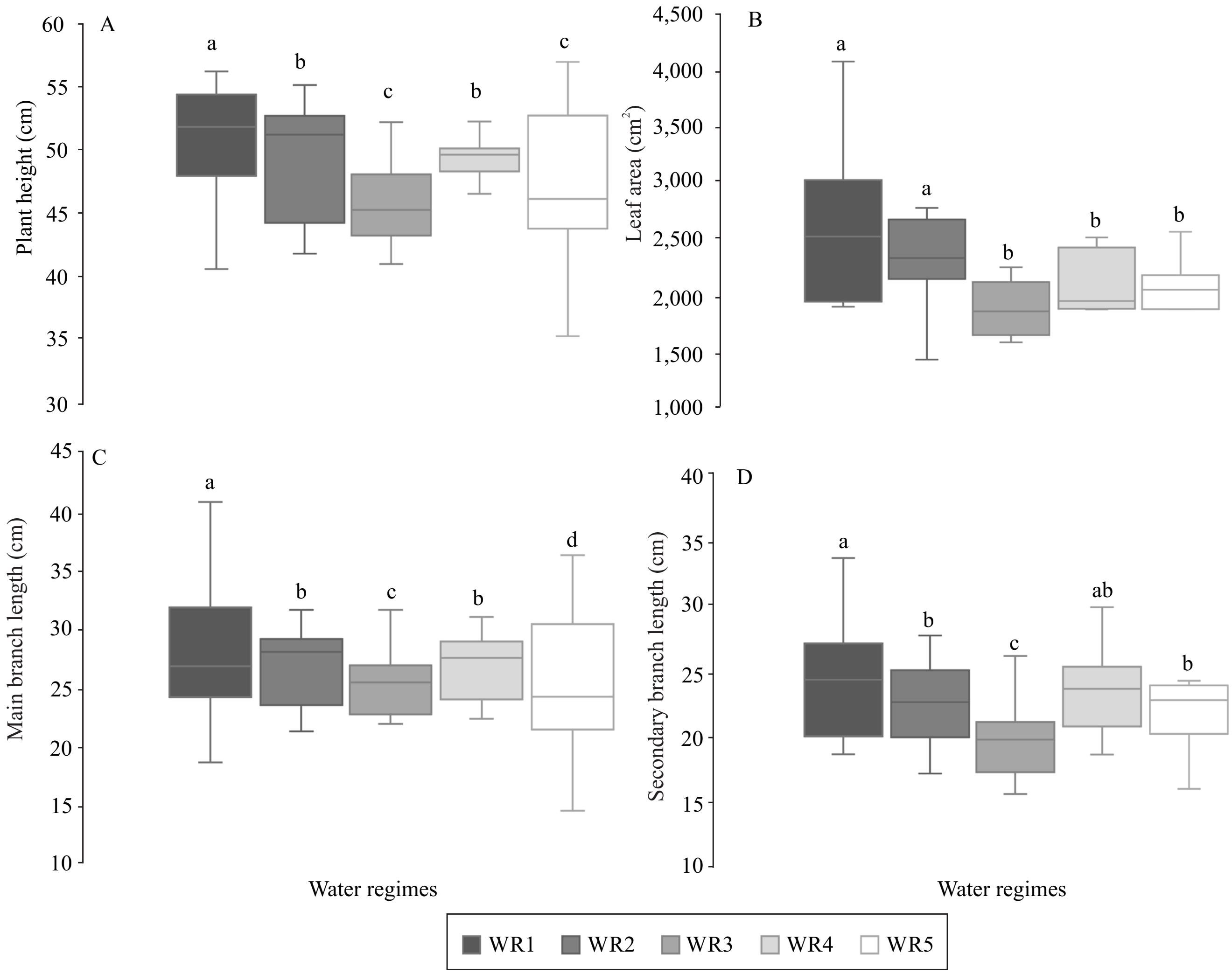

Figure 2. Plant height (A), leaf area (B), main branch length (C), and secondary branch length (D) of 'Ponkan' citrus (*Citrus reticulata*) plants grown under five water regimes (WR1–WR5) through three dehydration/rehydration cycles. WR1, WR2, and WR3, water regimes in which the plants were kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; and WR4 and WR5, water regimes in which the plants were kept at 75, 100, and 75% and 50, 100, and 50% of pot capacity during the first, second, and third cycles, respectively. Means (n = 120) followed by equal letters do not differ by the least significant difference test, at 5% probability.

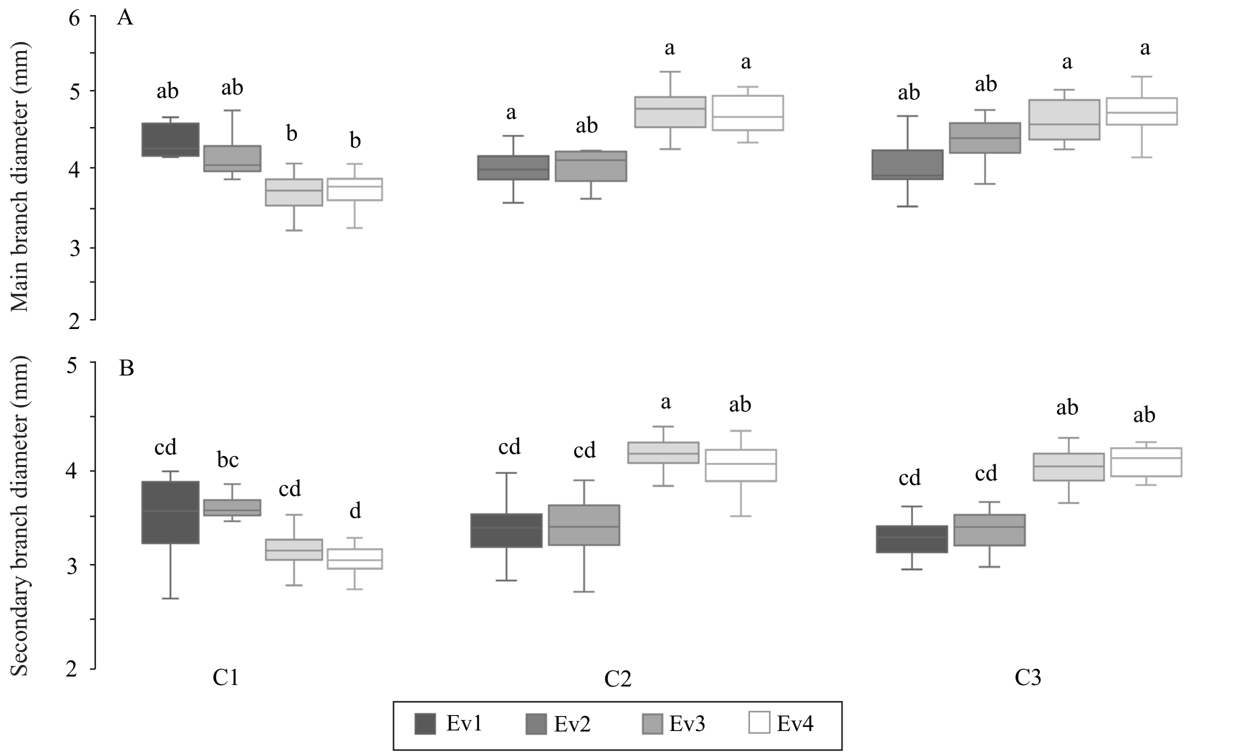

Figure 3. Main branch (A) and secondary branch (B) diameter of 'Ponkan' citrus (*Citrus reticulata*) plants grown under five water regimes and evaluated at four evaluation points (Ev1–Ev4) during three dehydration/rehydration cycles (C1–C3). Each dehydration/rehydration cycle lasted eight days, and the evaluation points were on the second (Ev1), fourth (Ev2), sixth (Ev3), and eighth (Ev4) day in each cycle. Means (n = 50) followed by equal letters do not differ by the least significant difference test, at 5% probability.

Table 1. Angle of leaf insertion in 'Ponkan' citrus (*Citrus reticulata*) plants grown under five water regimes (WR1–WR5) and evaluated at four evaluation points (Ev1–Ev4) during three dehydration/rehydration cycles (C1–C3)(1).

Factor	Angle of leaf insertion (°)				
	WR1	WR2	WR3	WR4	WR5
C1-Ev1	36.02±0.488	33.70±1.084	33.82±0.869	35.20±0.872	33.06±0.907
C1-Ev2	37.38±2.802	43.32±1.897	41.90±1.119	39.26±1.218	42.30±1.531
C1-Ev3	33.04±2.217	29.50±1.497	35.92±2.440	32.32±2.219	37.90±1.524
C1-Ev4	37.44±0.829	41.76±1.031	52.96±1.450	42.68±0.748	51.02±1.893
C2-Ev1	30.26±1.699	31.06±1.979	34.92±2.965	29.54±2.818	25.78±1.305
C2-Ev2	34.28±1.576	36.46±1.499	47.60±3.931	37.74±0.822	40.30±1.239
C2-Ev3	25.04±1.407	27.70±1.824	33.54±2.580	28.46±2.285	35.18±2.040
C2-Ev4	28.06±1.375	27.48±1.647	38.72±5.630	32.02±2.826	48.32±2.660
C3-Ev1	32.53±1.147	32.04±2.038	46.04±3.498	32.44±1.554	33.84±1.193
C3-Ev2	36.48±1.050	36.12±2.097	48.38±3.290	39.50±1.476	37.86±1.426
C3-Ev3	29.70±2.553	26.32±1.328	44.28±5.529	28.78±1.886	29.02±1.071
C3-Ev4	27.02±2.005	26.38±1.336	43.12±3.222	28.66±1.440	34.64±1.595

(1)C1, C2, and C3, each dehydration/rehydration cycle lasted eight days; Ev1, Ev2, Ev3, and Ev4, evaluations carried out on the second, fourth, sixth, and eighth day in each cycle, respectively; WR1, WR2, and WR3, water regimes in which the plants were kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; and WR4 and WR5, water regimes in which the plants were kept at 75, 100, and 75% and 50, 100, and 50% of pot capacity during the first, second, and third cycles, respectively. Values are reported as means ± standard error (n=10 for cycle x evaluation point x water regime).

with 50% of daily evapotranspiration (Table 1), which confirms the negative correlation observed between this variable and RWC (r = -0.85, p=0.066). Differences in leaf angle in response to factors such as water stress can result in a decrease in the radiation interception area, which, consequently, decreases leaf transpiration rate and heating, considered an adaptive response/advantage to water deficits that occurs when leaf transpiration increases and cells lose turgor pressure (Chutia & Borah, 2012; Singh et al., 2017). However, the plants in WR4 that reached RWC values of well-watered plants showed ALI values similar to those of the control treatment in the four evaluation points and three cycles. Furthermore, lower values were observed in the third cycle when compared with the first. This result suggests a lower loss of turgor pressure and an acclimatization process for ALI after exposure to successive events of dehydration/rehydration.

Considering the variables that were evaluated at the end of the experimental period, there was a significant effect of water regime on leaf dry matter ($F_{4.45}$ = 22.41, p<0.001) and branch dry matter ($F_{4,45}$ = 10.18, p<0.001), but not on SLA ($F_{4.45}$ = 1.62^{ns}) and leaf chlorophyll content ($F_{4.45}$ = 1.53^{ns}). Regarding leaf dry matter, WR1 showed the highest value, which decreased simultaneously with the water status of the regimes. In addition, WR2 and WR4 had higher values than WR3 and WR5 (Figure 4). For branch dry matter, a

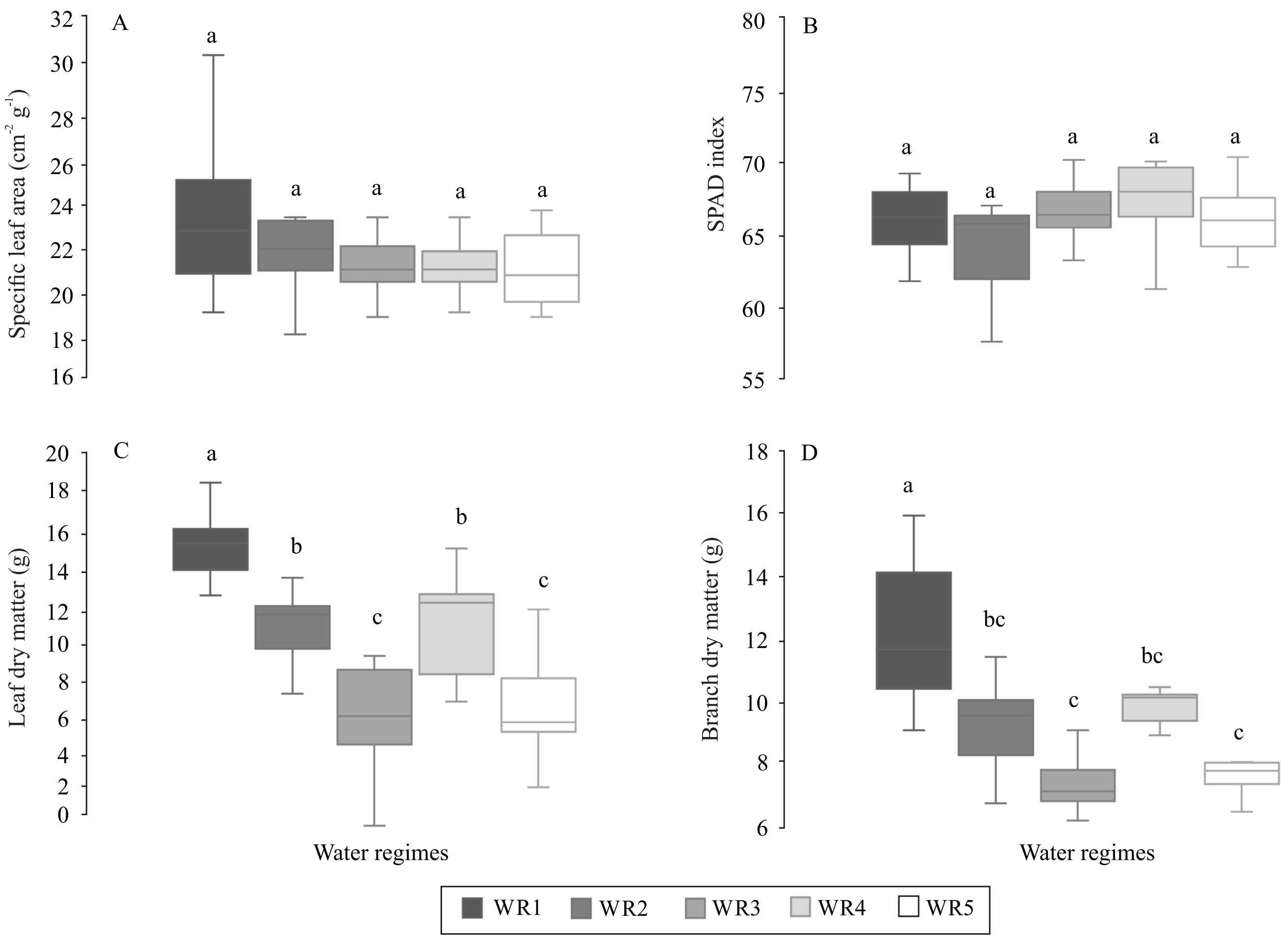

Figure 4. Specific leaf area (A), leaf chlorophyll content (B), leaf dry matter (C), and branch dry matter (D) of 'Ponkan' citrus plants (*Citrus reticulata*) grown under five water regimes (WR1–WR5) through three dehydration/rehydration cycles. WR1, WR2, and WR3, water regimes in which the plants were kept at 100, 75, and 50% of pot capacity during the three cycles, respectively; and WR4 and WR5, water regimes in which the plants were kept at 75, 100, and 75% and 50, 100, 50% of pot capacity during the first, second, and third cycles, respectively. Means (n = 10) followed by equal letters do not differ by the least significant difference test, at 5% probability.

similar trend was observed, with WR1 plants showing the highest values, which decreased, subsequently, depending on the percentage of reirrigation of the water regimes. Therefore, the accumulation of dry matter was positively correlated with the amount of water available, both for leaf dry matter (r = 0.9, p=0.037) and branch dry matter (r = 0.82, p=0.087).

Zaher-Ara et al. (2016) also found a significant reduction in citrus (*Citrus* spp.) dry weight when the level of water stress increased. Under stress conditions, in addition to the decrease in the photosynthetic process, the rate of leaf senescence increases and the investment in new leaves decreases to reduce the amount of area that transpires, leading to a lower dry matter accumulation (Fathi & Tari, 2016). The rehydration process restored the levels of dry matter accumulation to values higher than those of the related treatments without rewatering, i.e., leaf and branch dry matter values were higher in WR4, compared with WR2, and in WR5, compared with WR3. These results suggest that, for dry matter accumulation, the exposure to successive dehydration/rehydration events does not reflect acclimatization since rehydrated plants did not reach dry matter accumulation values equal to those of the well-hydrated plants in WR1.

Conclusions

1. Rehydration after a cycle with 50% of pot capacity does not improve plant growth or dry matter accumulation when compared with the well-hydrated control, but, after a cycle with 75% of pot capacity, water content, secondary branch diameter, and leaf insertion angle are restored.
2. The exposure to successive events of dehydration/rehydration alters subsequent plant responses.

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