MARÍLIA CECILIA DE SOUZA BITTENCOURT

RESPOSTAS FISIOLÓGICAS DE PIMENTEIRA ORNAMENTAL (*Capsicum chinense*) ENVASADA AO DEFICIT HÍDRICO E ÁCIDO ABSCÍSICO

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Fitotecnia, para obtenção do título de *Magister Scientiae*.

Orientador: Fernando Luiz Finger

Coorientadoras: Ariana Mota Pereira
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RESUMO

BITTENCOURT, Marília Cecilia de Souza, M.Sc., Universidade Federal de Viçosa, março de 2020. **Respostas fisiológicas de pimenteira ornamental (*Capsicum chinense*) envasada ao deficit hídrico e ácido abscísico**. Orientador: Fernando Luiz Finger. Coorientadoras: Ariana Mota Pereira e Paula Cristina Carvalho Lima.

O uso de meios de transporte inadequados na cadeia de produção e comercialização de plantas ornamentais pode gerar condições de elevada temperatura e baixa umidade, ocasionando estresse hídrico. A aplicação foliar de ácido abscísico (ABA) pode aumentar a tolerância das plantas a este estresse, no entanto, não há estudos do uso em pimenteiras ornamentais envasadas. Este trabalho teve como objetivo avaliar o efeito do deficit hídrico e aplicação de ABA sobre parâmetros fisiológicos e bioquímicos em pimenteiras ornamentais da cultivar biquinho (*Capsicum chinense*) na fase de pós-produção simulando transporte. O experimento foi instalado sob delineamento inteiramente casualizado, em esquema fatorial 2 x 2, sendo dois níveis de disponibilidade hídrica (irrigação até a capacidade de campo e deficit hídrico) e dois níveis de ABA (0 e 100 µM). Utilizou-se 5 repetições e cada unidade experimental foi constituída por um vaso com uma única planta. As avaliações foram realizadas antes e após a simulação do transporte, que ocorreu pelo acondicionamento das plantas em câmara B.O.D a 35 ± 2 °C e umidade relativa de 60-65%, por 20 horas. A análise estatística das épocas de avaliação foram consideradas como experimentos distintos. Os parâmetros avaliados foram: fotossíntese líquida (A), transpiração (E), condutância estomática (gs), concentração interna de CO_2 (Ci), eficiência do uso da água (A/E), pigmentos fotossintéticos (carotenoides, clorofila a, b e total), teor de malondialdeído (MDA), extravasamento de eletrólitos (EE), teor de prolina e teor relativo de água (TRA). A aplicação de ABA causou redução na gs somente nas plantas permanentemente irrigadas, acompanhada de uma redução na A após a simulação do transporte. Antes da simulação do transporte, independente da aplicação de ABA, a Ci foi menor sob deficit hídrico em comparação às irrigadas, enquanto após a simulação do transporte, apenas plantas não tratadas com ABA apresentaram menor Ci sob restrição hídrica quando comparadas às irrigadas. Antes da simulação do transporte, a aplicação de ABA estimulou o acúmulo de prolina em plantas sob deficit hídrico e promoveu menor EE tanto em plantas irrigadas quanto em plantas sob deficit. Após a simulação do transporte, a aplicação de ABA promoveu maiores níveis de carotenoides, clorofila a, clorofila b e clorofila total em plantas sob deficit hídrico.

Palavras-chave: Estresse hídrico. Fitormônio. Pimenteira biquinho.

ABSTRACT

BITTENCOURT, Marília Cecilia de Souza, M.Sc., Universidade Federal de Viçosa, March, 2020. **Physiological responses of potted ornamental pepper (*Capsicum chinense*) to water deficit and abscisic acid.** Adviser: Fernando Luiz Finger. Co-advisers: Ariana Mota Pereira and Paula Cristina Carvalho Lima.

The use of inadequate transport vehicles in the production and commercialization chains of ornamental plants can generate conditions of high temperature and low humidity, causing water stress. Foliar application of abscisic acid (ABA) can increase the tolerance of plants to this stress, however, there are no studies about its use on potted ornamental pepper. This work aimed to evaluate the effect of water deficit and application of ABA on physiological and biochemical parameters of 'Little beak' ornamental pepper plants (*Capsicum chinense*) in the post-production phase with transport simulation. The experiment was installed under a completely randomized design, in a 2 x 2 factorial scheme, with two levels of water availability (irrigation up to field capacity and water deficit) and two levels of ABA (0 and 100 μM). Five repetitions were used and each experimental unit consisted of a pot with a single plant. The evaluations were performed before and after the transport simulation, which occurred by conditioning the plants in a B.O.D chamber at 35 ± 2 ° C and relative humidity of 60-65%, for 20 hours. The statistical analysis of the evaluation periods was considered as different experiments. The parameters evaluated were: net photosynthesis (A), transpiration (E), stomatal conductance (gs), substomatal CO_2 concentration (Ci), water use efficiency (A/E), photosynthetic pigments (carotenoids, chlorophyll a, b and total), malondialdehyde (MDA) content, electrolyte leakage (EL), proline content and relative water content (RWC). The application of ABA caused a decrease in gs only in well-watered plants, accompanied by a reduction in A after transport simulation. Before transport simulation, regardless of ABA application, Ci was lower under water deficit compared to well-watered, while after transport simulation, only among plants not treated with ABA, a lower Ci was observed for those under water restriction. Before transport simulation, the application of ABA stimulated the accumulation of proline in plants under water deficit and provided lower electrolyte leakage (EE) both in plants under water deficit and in irrigated plants. After transport simulation, the application of ABA promoted higher levels of carotenoids, chlorophyll a, chlorophyll b and total chlorophyll in water-restricted plants.

Keywords: Drought stress. Phytohormones. Little beak pepper.

SUMMARY

1. **INTRODUCTION**

Ornamental peppers (*Capsicum* spp.) as potted plants are very popular in Europe (BOSLAND & VOTAVA, 1999) and are gaining in popularity in the Brazilian market, with great expansion perspectives (RÊGO *et al.*, 2011). The increasing interest in ornamental peppers can be attributed to their high aesthetic value characteristics (such as plant architecture; quantity, shape and color of the fruits; color, shape and density of the leaves), the easy propagation and cultivation, the ability to grow in containers as perennial plants and for presenting a long shelf life (NEITZKE, 2016).

Edible landscaping, the use of food plants as design features in a landscape, has been a gardening trend in recent years. Thus, the demand for ornamental peppers with low pungency fruits has increased, such as the ‘Biquinho’ pepper (PINTO *et al.*, 2012), one of the most cultivated and consumed varieties in Brazil (CARVALHO *et al.*, 2006). ‘Biquinho’ pepper is a botanical variety of *C. chinense*, the species most often grown in Brazil, being the Amazon basin its main center of diversity (BOSLAND & VOTAVA, 1999).

In Brazil, important bottlenecks occur on the ornamental plants supply chain, such as inadequate transport facilities, without thermal insulation, ventilation, lighting and irrigation systems, generating a high temperature and low humidity environment (JUNQUEIRA & PEETZ, 2008) and, consequently, leading to drought stress conditions, which causes yellowing, withering and abscission of leaves and flowers (PINTO *et al.*, 2012).

Drought stress induces a series of physiological and biochemical changes in plants, such as reduced leaf expansion, stomatal closure, photosynthetic inhibition, production of reactive oxygen species (ROS), ionic cytotoxicity, among others (FAROOQ *et al.*, 2009), leading to reduced quality and shorter shelf life of ornamental potted plants.

Among the hormones involved in plant responses to drought stress, there is abscisic acid (ABA), a 15-carbon terpene synthesized from carotenoids in plastids - chloroplasts or amyloplasts (MITSUNORI & KOSHIBA, 2002). ABA is recognized as the “stress hormone”, given its rapid accumulation under conditions of water deficiency (DAVIES & ZHANG, 1991) and other abiotic stresses, such as saline and thermal stresses (LEUNG & GIRAUDAT, 1998). Under drought stress, ABA concentration in leaves can increase about 50 times in 4 to 8 hours (TAIZ *et al.*, 2017).

The increase in ABA levels in drought-stressed plants triggers a signaling cascade to close stomata and, consequently, reduce water loss via transpiration (MUNEMASA *et al.*, 2015). However, stomatal closure also restricts the diffusion of CO_2 into the leaves, a limiting factor for photosynthetic performance (MEDINA *et al.*, 1999). In addition to its primary role in stomatal regulation, there is accumulating evidence that abscisic acid plays an important part in the expression of genes (SHINOZAKI & YAMAGUCHI-SHINOZAKI, 2000; ALAMILLO & BARTELS, 2001) and other metabolic changes (AGARWAL *et al.*, 2005) that contribute to mitigate the damages caused by drought stress.

Several authors have suggested that the application of ABA in drought-stressed plants promotes the efficiency of water use (YANG *et al.*, 2016), increases the concentration of antioxidant enzymes (CHOUDHARY *et al.*, 2012), increases the levels of photosynthetic pigments (SANKAR *et al.*, 2013) and maintains membrane stability and leaf water status (LI *et al.*, 2016). Thus, this hormone has great potential in mitigating the damaging effects of water deficiency in cultivated plants, and may become an important technology in maintaining the quality of agricultural products, including ornamental potted plants.

The aim of this work was to determine the effect of water deficit and application of ABA on physiological and biochemical parameters in potted ornamental pepper.

2. MATERIALS AND METHODS

2.1 Plant growth and treatment conditions

The plants were grown in a greenhouse, located at the Federal University of Viçosa (UFV), in the city of Viçosa, MG. Seeds of biquinho pepper (Top Seed®) were planted in a 128 cells polystyrene seedling tray containing commercial substrate (Tropstrato HT Hortaliças®). When presenting 4 to 6 true leaves, the seedlings were transplanted to 760 ml pots, filled with the same commercial substrate used for planting.

The following cultural treatments were carried out: (i) manual weed removal; (ii) biweekly fertigation until the beginning of fruiting, with the concentrated liquid fertilizer B&G® (6-8-6 NPK + Ca, Mg, S, B, Fe, Mn and Zn); (iii) pest and disease control and (iv) daily irrigation, from sowing to the installation of the experiment.

When the plants reached the commercialization point, that is, 50% of the population's plants with at least 30% of its fruits ripe (RIBEIRO *et al.*, 2015), the foliage was sprayed until runoff with aqueous solution of 0 and 100 µM ABA, with 20 plants per ABA treatment. Drought stress was applied to half of the plants for each ABA treatment, beginning after the application of the phytohormone by withholding water for 2 consecutive days. Plants in the non-stressed control treatment received enough water to fully saturate soil daily. Plants in the 0 µM ABA treatment were sprayed with water only.

To prepare the 100 µM ABA solution, the synthetic hormone (Sigma-Aldrich®) was diluted in water, with the addition of 0.2% of the non-ionic surfactant Tween 20®. The application was carried out via manual spraying and to avoid drift each plant was sprayed individually in an isolated location.

The plants were evaluated at two different times, before and after the transport simulation. The transport simulation took place at the UFV Horticulture Post-Harvest Physiology Laboratory through the conditioning of the plants in a B.O.D. for 20 hours, in the dark, at 35 ± 2 ° C and relative humidity of 60-65%.

Gas exchange parameters were evaluated on intact plants at 2 days after the initiation of watering treatments as described below. Following these measurements, the most fully expanded leaves from each plant were removed for determination of relative water content. The remaining expanded leaves were removed and rapidly frozen in liquid nitrogen to be used for all other analyses as described below.

2.2 Gas exchanges

Net photosynthesis (A), transpiration (E), stomatal conductance (gs) and substomatal CO_2 concentration (Ci) were measured using an Infrared Gas Analyzer (IRGA), model LI 6400XT LI-COR®. Measurements were made on the middlemost fully expanded leaves along the plant vertical axis. Instantaneous water use efficiency was calculated as the ration of net photosynthetic rate to transpiration rate (A/E). The environmental conditions in which these measurements were made were: 2,594 kJ m^{-2} of radiation, average temperature of 20 °C and average relative humidity of 60%.

2.3 Chlorophyll and carotenoid concentration

Leaf chlorophyll and carotenoid concentrations were determined according to the method described by Dere *et al.* (1998), with modifications. Approximately 0.4 g of the freeze-leaf sample was weighed and macerated under low light conditions. The pigments were extracted from leaf tissues using 2 ml of 95% methanol. After maceration and filtering, the filter paper was washed with methanol and the volume adjusted in a 25 ml volumetric flask. The absorbance of the extract was measured at 666, 653 and 470 nm, using the Genesys 10S UV-VIS spectrophotometer. The formulas used in the calculation of the pigments concentration, in µg/mL, proposed by Lichtenthaler and Wellburn (1983), were as follows, the result being converted and expressed in mg.100 g^{-1} of fresh mass:

Chlorophyll *a* (C*a*): $15{,}65\ A_{666} - 7{,}34\ A_{653}$

Chlorophyll *b*(C*b*): $27{,}05A_{653} - 11{,}21\ A_{666}$

Total Chlorophyll: (C*a*) + (C*b*)

Carotenoids: $1000\ A_{470} - 2{,}860\ (Ca) - 129{,}2\ (Cb)/\ 245$

2.4 Malondialdehyde

The malondialdehyde (MDA) content was determined according to the methodology proposed by Heath and Packer (1968). The freeze-leaf sample (200 mg) was macerated in 2 ml of trichloroacetic acid (1% w/v TCA) using previously cooled mortar and pistils. The homogenate was centrifuged at 12,000 g for 15 minutes at 4 ºC. In new eppendorfs, 1.5 ml of thiobarbituric acid + trichloroacetic acid (0.5% TBA + 20% TCA, w/v) were added together with 500 µL of the supernatant (macerated and centrifuged extract). The sample was incubated in a water bath at 90 ºC for 20 minutes and then centrifuged at 3,000 g for 4 minutes. The absorbance of the sample was measured at 532 and 600 nm, using the Genesys 10S UV-VIS spectrophotometer. The formula used in calculating the MDA was:

$$\text{MDA (nmol ml}^{-1}) = [(A_{532}\text{-}A_{600})/155000]\ 10^{6}$$

2.5 Electrolyte leakage

Electrolyte leakage was determined as described by Lima *et al*. (2002). Five leaf discs obtained from fresh leaf tissues were thoroughly washed with running water and subsequently floated on 10 ml of deionized water in sealed vials. The electrical conductivity of the liquid containing the disks was measured in a portable conductivity meter after incubation at room temperature for 6 hours (Ci: initial conductivity) and again after incubation in an oven at 90 ºC for 2 hours (Cf: final conductivity). The electrolyte leakage was expressed as the percentage of conductivity in relation to the total conductivity after treatment for 2 hours at 90 ºC, according to the following formula: [(Ci / Cf) x 100)].

2.6 Proline concentration

Proline concentration was determined according to the methodology proposed by Bates *et al.* (1973), with modifications. Approximately 100 mg of freeze-leaf sample was macerated using 3% sulfosalicylic acid (3 ml) as a solvent and the extract was centrifuged for 10 minutes at 2,000 g. The supernatant (1 ml) was removed and mixed with equal volumes of acid ninhydrin reagent and glacial acetic acid and then heated in a water bath for 1 hour at 100 °C. After heating, the solution was cooled in an ice bath and the absorbance was measured at 520 nm, using the Genesys 10S UV-VIS spectrophotometer. Proline concentration was determined against a standard curve and expressed as µmol g^{-1} of fresh mass.

2.7 Relative water content

Relative water content (RWC) was determined according to the methodology proposed by Turner (1981), with modifications. Leaf discs (10) were cut from the most fully expanded leaves and immediately weighted on a precision balance to obtain fresh weight (FW). Turgid leaf weights (TW) were determined after incubating leaf discs in deionized water in Petri dishes for 24 hours. Leaf dry weights (DW) were determined after drying leaf discs at 65°C for 2 days. RWC was calculated using the formula:

$RWC = [(FW – DW)/(TW – DW)] \times 100$.

2.8 Statistical analysis

The experiment was installed under a completely randomized design, in a 2 x 2 factorial scheme, with two levels of water availability (irrigation and water deficit) and two levels of ABA (0 and 100 µM). Five repetitions were used and each experimental unit consisted of a pot with a single plant. The statistical analyses of the two evaluation periods were considered as different experiments. The data obtained were subjected to analysis of variance at 5% probability. Regardless of the significance of the F test for interaction, it was decided to split the effects of the factors under study. Statistical analyzes were performed using the software R (R TEAM, 2017).

3. RESULTS AND DISCUSSION

3.1 Gas exchanges

Before transport simulation, there was no significant difference between treatments for variables A and E (Figure 1). Thus, it is concluded that the Biquinho ornamental pepper did not show any changes in these parameters under this water deficit intensity and that exogenous ABA did not cause a significant effect on these variables.

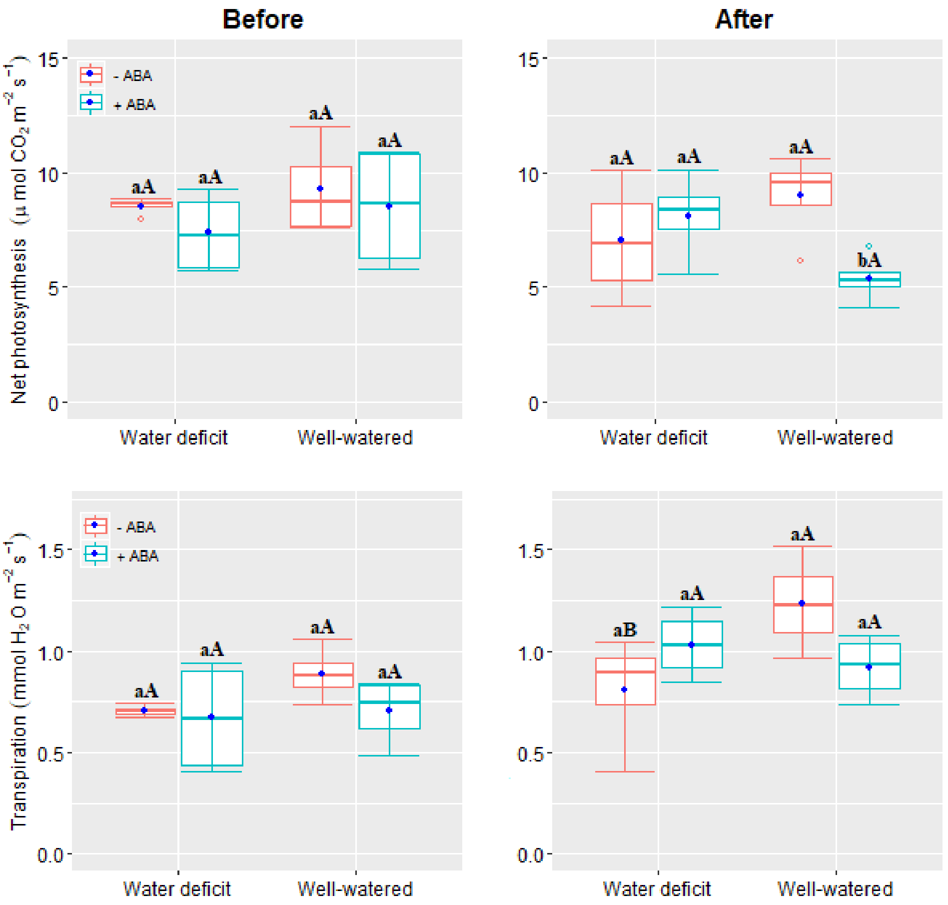

Figure 1 - Net photosynthesis (A) and transpiration (E) of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

The absence of significant variation for A and E before transport simulation, after 2 days of the suspension of irrigation, suggests that the intensity of water stress imposed was not sufficient to trigger a broad stomatal closure, which would reduce transpiration as well as hamper photosynthesis. Furthermore, the conduction of the experiment in a greenhouse, as well as the mild climatic conditions verified during the evaluation of the plants, a period in which the average temperature and relative humidity of the air were 20 °C and 60%, respectively, possibly had an influence on the results obtained in the present study, by reducing the plants water requirements.

Regarding stomatal conductance before transport simulation, there were significant differences between treatments (Figure 2). In irrigated plants, gs was lower in those treated with ABA compared to those that did not receive the hormone, representing a difference of 28.9%. On the other hand, regardless of the application of ABA, gs was 42% lower under water deficit compared to irrigation. As it can be seen in Figure 2, irrigated plants supplied with ABA exhibited a similar response in stomatal conductance compared with that of plants under water deficit condition with or without exogenous ABA. Pacheco (2007) reported that ABA application at 100 μM on regularly irrigated pot marigold (*Calendula officinalis* L.) reduced the stomatal conductance the same way water deficit did in drought-stressed plants. These results suggest that ABA treatment might induce stomatal closure in well-watered plants and thus, substitute endogenous ABA synthesis.

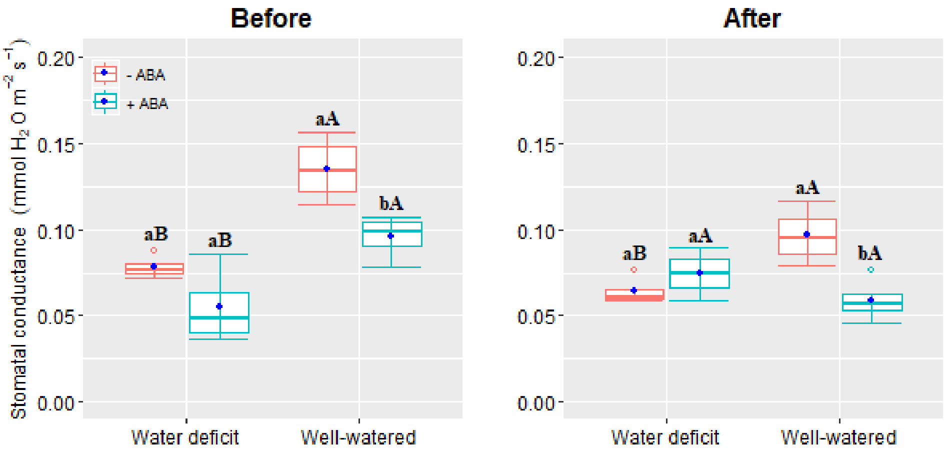

Figure 2 - Stomatal conductance (gs) of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

After transport simulation, among the irrigated plants, the photosynthetic rate and stomatal conductance were, respectively, 40.3% and 39.2% lower in those treated with ABA compared to those not treated with the hormone (Figure 1). It can be observed that decreased values in gs were accompanied by decreased values in A, thus it appears that the lower photosynthetic rate observed in irrigated plants treated with ABA is mainly due to stomatal limitation as a result of ABA application.

Regarding transpiration after transport simulation, among ABA non-treated plants, those under water deficit presented a rate 34.1% lower than those irrigated (Figure 1). Similarly, the stomatal conductance of plants not treated with ABA was 34.0% lower under water restriction compared to irrigation (Figure 1). As it can be noted, E and gs present roughly the same percentage of reduction in water-restricted plants compared to irrigated, suggesting that stomatal limitation is the main factor restraining transpiration in plants under water deficit, possibly involving ABA synthesis responses.

Instantaneous water use efficiency did not show significant differences in response to ABA application and suspension of irrigation both before and after transport simulation (Table 1).

Table 1 - Water use efficiency (A/E) of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation.

	Water use efficiency (A/E)			
	Before		**After**	
	Water deficit	Well-watered	Water deficit	Well-watered
+ ABA	324.88 aA	398.31 aA	208.67 aA	265.74 aA
- ABA	300.21 aA	298.08 aA	267.66 aA	198.54 aA
CV (%)	**32.32**		**32.73**	

* Means followed by the same lowercase letter in the column or uppercase letter in the row do not differ by the F test at 5% probability.

Photosynthetic or instantaneous water-use efficiency can be defined as the ratio of CO_2 assimilation into the photosynthetic biochemistry (A) to water lost, via transpiration (E), through the stomata (BACON, 2004). Thus, it is clear that the regulation of stomatal aperture is central to the water use efficiency of plants. In the present study, although some changes were observed in gs both before and after transport simulation, A and E remained statistically equal between treatments before transport simulation, with some changes after the simulation. Thus, as A and E were not greatly affected by ABA application and water deficit, so was not their ratio (A/E). The consequences of water stress on vegetables are very varied and depend on the intensity, as well as the duration of the stress to which the plant is being subjected (MENDES *et al.*, 2007). Pacheco *et al.* (2011) reported no influence of water deficit and ABA application on instantaneous water use efficiency of potted marigold until 9 days after total suspension of irrigation.

For the substomatal CO_2 concentration (Ci), differences were observed both before and after transport simulation (Figure 3). Before transport simulation, regardless of the ABA application, Ci was lower under water deficit compared to irrigation, whilst after transport simulation, only among plants not treated with ABA, a significant lower Ci was observed for those under water restriction compared to irrigated. The lower supply of CO_2 into the leaves of plants under water deficit is presumably related to endogenous ABA synthesis, induced by stress, which in turn acts on stomatal closure. Water deficit is one of the main challenges faced by farmers, especially in water-scarce regions, and it triggers various responses in plants, such as stomatal closure that reduces stomatal conductance thus reducing the internal CO_2 concentration (HONG-BO, 2008).

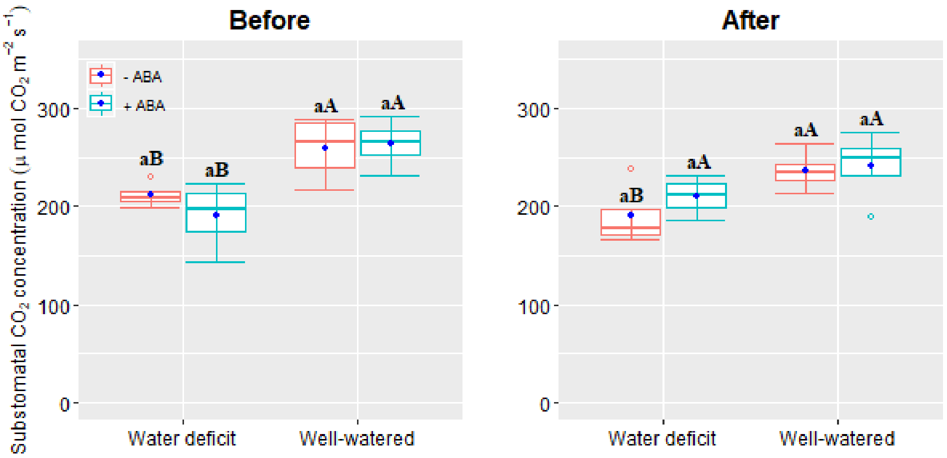

Figure 3 - Substomatal CO_2 concentration (Ci) of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

When evaluating the unfolding of ABA levels for each level of water availability, it is observed that the application of ABA did not have an effect on any of the variables in plants under water restriction, while plants that were permanently irrigated showed lower values of gs when treated with the hormone, both before and after transport simulation (Figure 2). The lack of response to exogenous ABA in water-restricted plants might be related to the application method. It is known that foliarly applied ABA is not readily absorbed in contrast to a root drench application (RAO; RAGHAVENDRA; REDDY, 2006). In addition to the lower absorptive capacity of leaves, the suspension of irrigation that followed ABA spraying might have hampered translocation of the hormone through the xylem. Other possibilities for lack of response to ABA is degradation, sequestration and unavailability of ABA binding sites (RAO; RAGHAVENDRA; REDDY, 2006).

3.2 Photosynthetic pigments

Before transport simulation, irrigated plants treated with ABA presented 48.3%, 47.6% and 51.9%, higher levels of chlorophyll a, chlorophyll b and total chlorophyll, respectively, compared with irrigated ABA non-treated plants (Figure 4). Among the plants that were not treated with ABA, higher levels of pigments were observed in those under water restriction, which had 45.8%, 45.0% and 45.6% higher levels of chlorophyll a, chlorophyll b and total chlorophyll, respectively, in relation to irrigated ones (Figure 4).

After transport simulation, water-restricted plants treated with ABA had 37.3%, 43.3% and 39.1% higher levels of chlorophyll a, b and total, respectively, when compared to ABA non-treated plants (Figure 4). Among the plants that did not receive ABA, those normally irrigated had 37.7% and 34.5% higher contents of chlorophyll a and total chlorophyll, respectively, than water-restricted ones (Figure 4).

Before transport simulation, there was no difference between the studied factors for the carotenoid content, whereas after transport simulation, water-restricted plants treated with ABA presented a 45.3% higher carotenoid content than non-treated ones (Figure 5).

According to Jaleel *et al*. (2009), the leaf content of photosynthetic pigments in plants under drought stress conditions is reduced due to oxidative damage. However, it appears that the decrease in chlorophyll contents is more frequent under severe stress (MASSACCI *et al*., 2008; KIANI *et al*., 2008; LUÍS, 2009), which could explain the contrasting results obtained before and after transport simulation. At 2 days of suspension of irrigation, before transport simulation, the water deficit imposed was not sufficient to cause decreases in the levels of leaf chlorophyll and, conversely, lower concentrations were observed in plants under constant irrigation. After transport simulation at 35 °C for 20 hours, totaling 3 days of irrigation suspension, water-restricted plants not treated with ABA showed, on average, the lowest levels of chlorophyll, possibly due to the longer exposure time to stress, thus intensifying its severity, and because they have been kept in the dark, a condition that stimulates the degradation of photosynthetic pigments (OKADA *et al*., 1992).

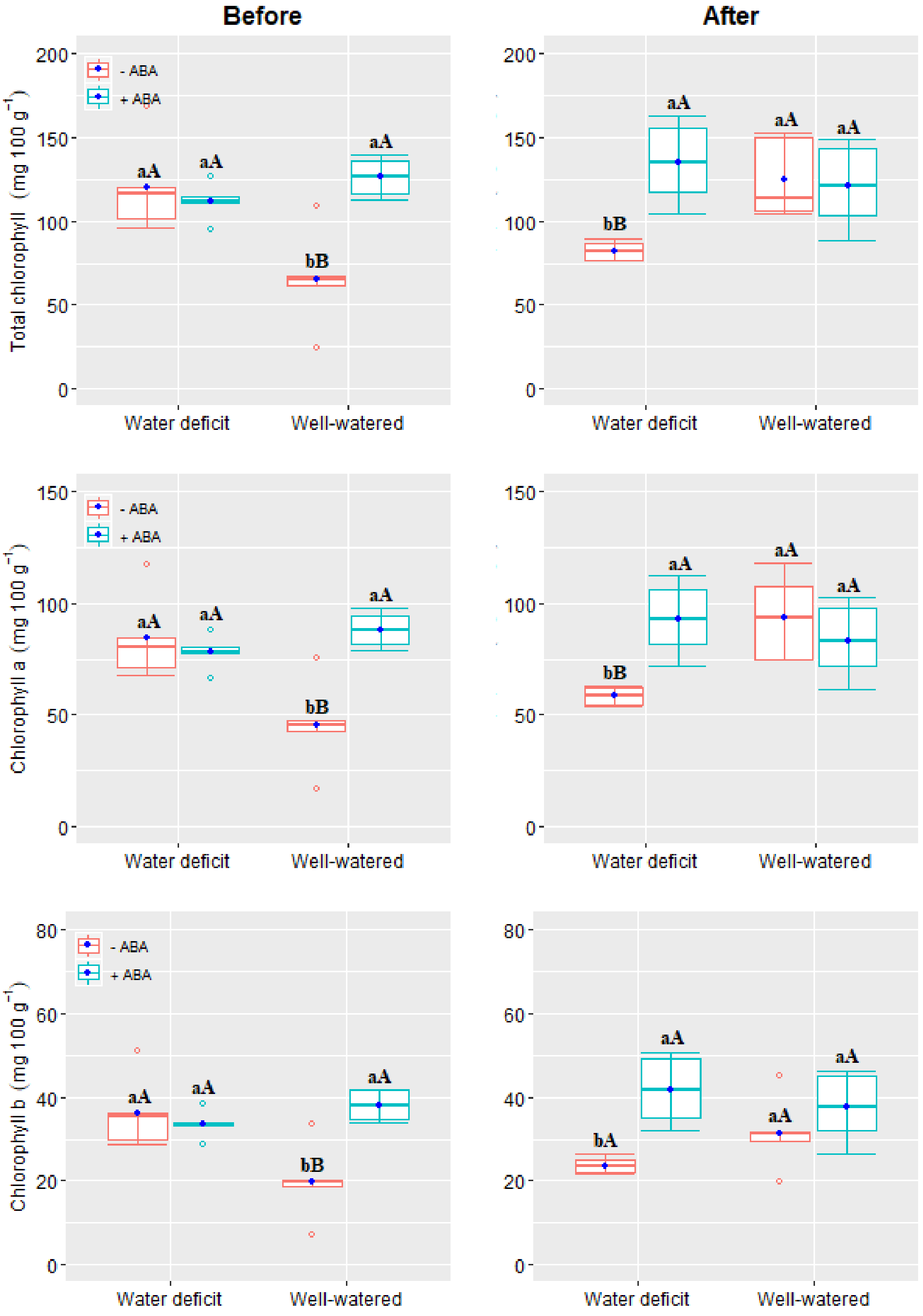

Figure 4 - Total chlorophyll, chlorophyll a and chlorophyll b of Biquinho ornamental pepper leaves as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the

median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

Figure 5 - Leaf carotenoid concentration of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

According to Travaglia *et al.* (2007; 2010), the application of ABA maintains or increases the levels of chlorophyll a and b in drought-stressed plants and, thus, slows the senescence of the leaves, which remain green for a longer time. In addition, with the use of the hormone there is also an increase in carotenoid levels, which contribute to maintaining the integrity of the photosynthetic apparatus, since theses pigments indirectly reduce the formation of reactive oxygen species (FOYER & HARBINSON, 1994). The results obtained in the present study corroborate with the aforementioned statements, since, after transport simulation, both the content of chlorophyll a, b and total, and that of carotenoids, was higher in water-restricted plants treated with ABA compared to those not treated with the hormone.

3.3 Cell membrane damage

Before transport simulation, there was no significant difference between the studied factors for the malondialdehyde content (Figure 6). Thus, it is concluded that the Biquinho pepper did not show any changes in this parameter under this water deficit intensity and that exogenous ABA did not cause a significant effect as well.

Drought stress promotes intense production of reactive oxygen species (ROS) as a consequence of decoupling of photosystems induced by dehydration, thus leading to oxidative stress. The main cellular components susceptible to damage by ROS are membrane lipids (MATTOS & MORETTI, 2015). Malondialdehyde is one of the secondary products of lipid peroxidation and, therefore, an important biomarker in the detection of oxidative stress in biological samples (DRAPER & HADLEY, 1990). According to Jiang and Zhang (2002b), oxidative stress is only observed in plants under severe drought conditions. Sgherri *et al.* (1993) and Esfandiari *et al.* (2007) report that the intensity of oxidative damage to cell membranes is positively correlated with the intensity of drought stress imposed, which would explain the absence of a significant effect for MDA before transport simulation, at two days of water restriction.

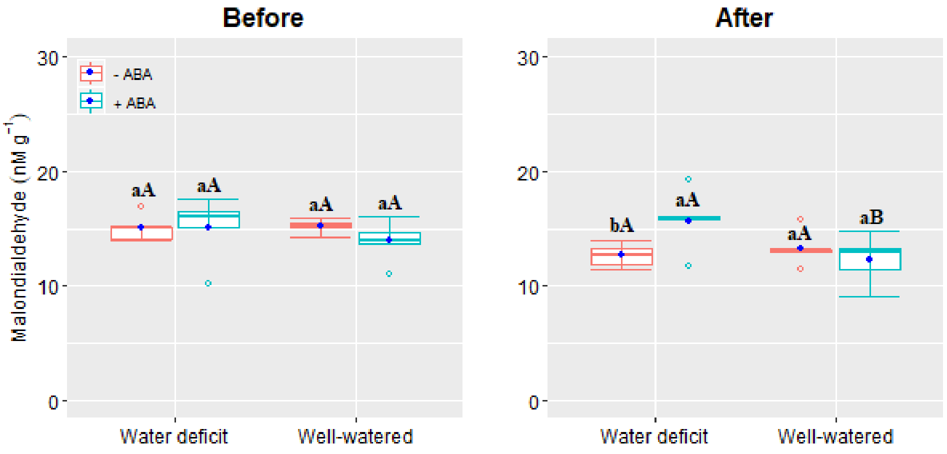

Figure 6 - Malondialdehyde level (MDA) of Biquinho ornamental pepper leaves as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

After transport simulation, water-restricted plants treated with ABA presented a higher MDA content than those not treated, corresponding to a difference of 19.3% (Figure 6). Also, among ABA-treated plants, a 21.8% higher MDA content was observed in those under water restriction compared to irrigated (Figure 6).

Some studies have shown that plants under abiotic stresses, including drought, pre-treated with ABA may show a reduction in MDA levels, when compared to untreated ones (KURCHII, 2002; GUO *et al.*, 2012). The mitigation of membrane damage promoted by this hormone is partly related to the improvement in the plant's antioxidant defense system, which prevents the accumulation of ROS (JIANG & ZHANG, 2002b). However, this effect is not always observed, as verified by Travaglia *et al*. (2010) in wheat, where pre-treatment with ABA did not alter the levels of MDA in plants under different water regimes.

In the present study, water-restricted plants treated with ABA showed, on average, the highest levels of MDA. According to Pacheco (2007), the ABA's action on the closure of stomata is rapid, generally occuring even before the total increase in ABA concentration in response to drought stress. Thus, it is suggested that the water restriction imposed associated with the application of ABA led to a quickly closure of stomata, with consequent accumulation of ROS and, however, due to the short interval between the application of the hormone and the evaluation of the plants, it has not been able to act in the removal of the formed ROS or in the repair of its damage.

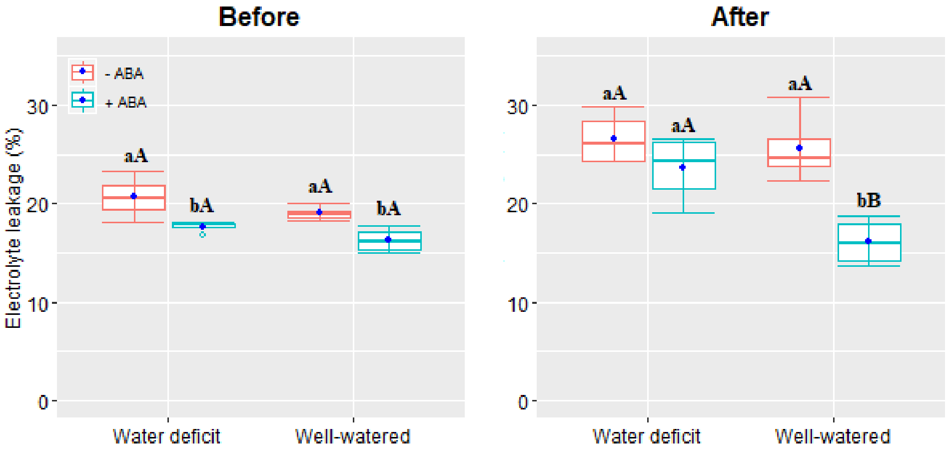

Figure 7 - Electrolyte leakage (EL) of Biquinho ornamental pepper leaves as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

Before transport simulation, regardless of water availability, the EL was 14.5% lower in ABA-treated plants (Figure 7). After transport simulation, irrigated plants treated with ABA presented a 37.3% lower EL compared to untreated ones. Also, among ABA-treated plants, the EL was 31.7% lower in those irrigated compared to water-restricted (Figure 7).

Measurement of electrolyte leakage is another important cell membrane damage indicator, since the loss of membrane integrity leads to the passage of solutes from the inside to the outside of the cells (BERRY & BJORKMAN, 1980). Before transport simulation, the suspension of irrigation for 2 days did not affect the permeability of the membranes, based on the EL, probably due to the slight intensity of water stress imposed. During transport simulation plants were exposed to a higher temperature (35±2 °C) for 20 hours, which probably lead to an increase in the fluidity of cell membranes, promoting greater electrolyte leakage, except for irrigated ABA-treated plants.

The relationship between cell membrane permeability, estimated by EL, and ABA is still unclear. Depending on the species and cultivation conditions, ABA may not have an effect or be associated with both increases and decreases in membrane permeability (TAN & BLAKE, 1993). Jiang and Zhang (2002a) reported that ABA treatment did not change the percentage of EL in leaves of drought-stressed maize. On the other hand, Wang *et al.* (2003) verified that *Poa pratensis* plants pre-treated with ABA and exposed to drought stress had greater membrane stability, as indicated by the lower EL in the leaves. However, these authors also observed that EL was not affected by the application of ABA in well-hydrated plants, contrary to what was verified in the present study.

The results presented here show that the application of ABA provided lower EL both in water-restricted and in irrigated plants, suggesting that the hormone is capable of reducing the damage caused by dehydration by protecting cell membranes, as well as acting in their stabilization under optimal water supply conditions.

3.4 Proline concentration and relative water content

For the concentration of proline, differences were observed both before and after transport simulation (Figure 8). Before transport simulation, among ABA-treated plants, proline content was 25.9% higher in water-restricted ones compared to irrigated. Also, after transport simulation, among the plants that were not treated with ABA, those under water restriction presented a 38.6% higher proline concentration than irrigated ones. These results corroborate with the findings of several authors that report proline accumulation in drought-stressed plants, such as *Beta vulgaris* (FUGATE *et al.*, 2018), *Eugenia uniflora* and *Photinia* x *fraseri* Dress 'Red Robin' (TOSCANO *et al.*, 2016).

Before transport simulation, water-restricted plants treated with ABA presented a 42.5% higher proline content than those non-treated. Contrarily, after transport simulation, proline content of plants under water deficit that received exogenous ABA was 36.6% lower than those not treated with the hormone.

Apparently, proline accumulation in plants under drought stress is mediated by both ABA dependent and independent signaling pathways (HARE *et al*., 1999). Some authors have verified increases in proline levels in ABA-treated plants, such as barley and pea (HASSON & POLJAKOFF-MAYBER, 1983; STEWART, 1980; STEWART & VOETBERG, 1985). On the other hand, the application of ABA did not induce increased proline levels in maize plants (DALLMIER & STEWART 1992) and *Spinacia* or *Pennisetum* seedlings (McDONNELL *et al*., 1983). Based on what was previously exposed, it is not possible to establish a clear relationship between the exogenous application of ABA and the accumulation of proline in plants under water restriction.

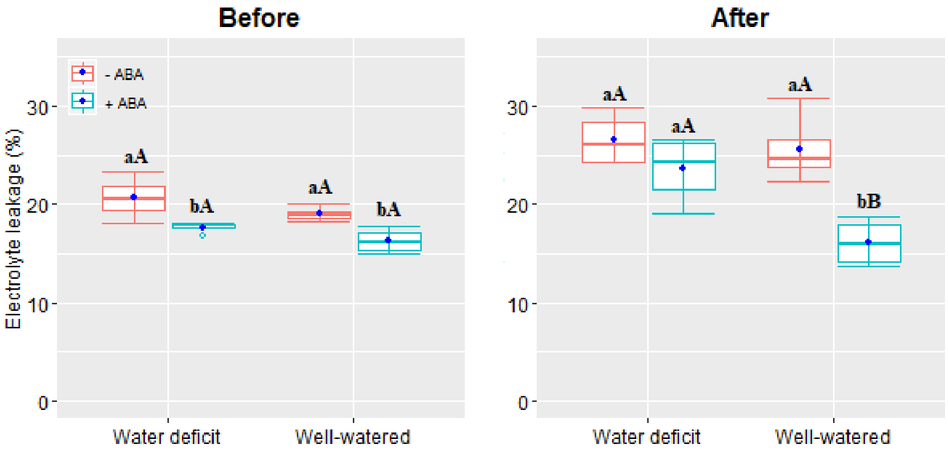

Figure 8 - Leaf proline concentration of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

As it can be observed in Figure 8, proline levels before transport simulation were, on average, higher than 1.0 mM g^{-1}, while after transport simulation they were lower than 1.0 mM g^{-1}, even though water deficit at this point was more intense (3 days of water restriction). In a study with *Arabidopsis*, the induction of proline accumulation by salt stress was inhibited in plants subjected to dark treatment, suggesting that light plays an important role in regulating the biosynthesis of this amino acid (ÁBRAHÁM *et al*., 2003). Therefore, the simulation of transport for 20 hours in the dark may have interfered with the synthesis and accumulation of proline.

Before transport simulation, at two days of water restriction, the water deficit imposed was not sufficient to cause major changes in the RWC of Biquinho pepper plants, as well as the applied ABA was not able to cause any effect on this parameter (Figure 9). However, a small, although statistically significant difference was observed after transport simulation, among ABA-treated plants, where RWC was 3.1% lower under water restriction (87,11%) compared to irrigation (89,88%) (Figure 9), which is justified by the irrigation suspension treatment. Possibly, the maintenance of the RWC was only due to the stomatal control of the plant and the likely endogenous ABA induced by water restriction, and the application of supplementary ABA does not seem to have had any effect.

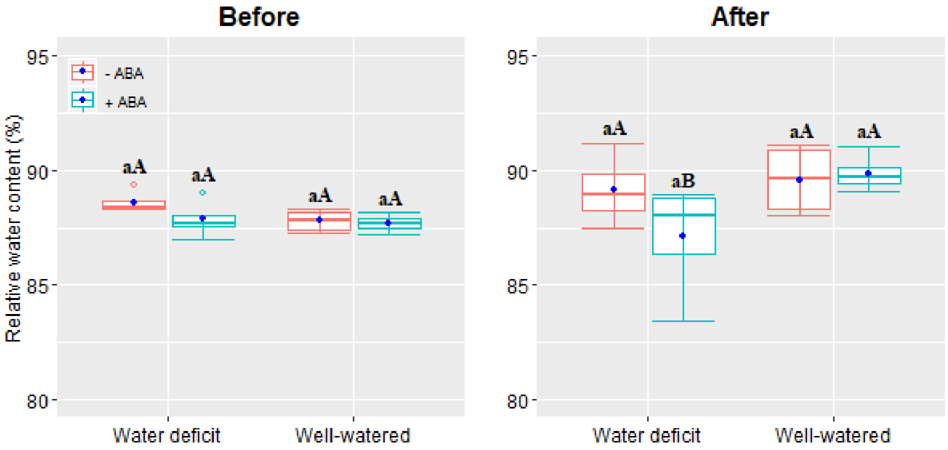

Figure 9 - Relative water content of Biquinho ornamental pepper as affected by water deficit and ABA application before and after transport simulation. Lower case letters compare the levels of ABA within each level of water availability, and capital letters compare the levels of water availability within each level of ABA. Boxes represent the median, first and third quartiles. Blue circle represents the mean (n = 5). Means followed by the same letter do not differ by the F test at 5% probability.

Pacheco (2007) also reported no significant changes in the RWC of potted marigold plants at 6 days of water restriction, treated or not with ABA. According to this author, the absence of variation in the RWC can be explained by an osmotic adjustment of the plant itself as an adaptive response during periods of drought.

4. CONCLUSIONS

The exogenous application of ABA on the gas exchanges had the main effect of causing a decrease in stomatal conductance (gs) only in well-watered plants, accompanied by a reduction in net photosynthesis (A) after transport simulation. Also, before transport simulation, regardless of ABA application, substomatal CO_2 concentration (Ci) was lower under water deficit compared to well-watered, while after transport simulation, only among plants not treated with ABA, a lower Ci was observed for those under water restriction.

Before transport simulation, the application of ABA stimulated the accumulation of proline in plants under water deficit and provided lower electrolyte leakage (EE) both in plants under water deficit and in irrigated plants.

After transport simulation, the application of ABA promoted higher levels of carotenoids, chlorophyll a, chlorophyll b and total chlorophyll in water-restricted plants.

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