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Physiological response of black pepper (*Piper nigrum* L.) to deficit irrigation[1]

Resposta fisiológica da pimenta-do-reino (*Piper nigrum* L.) ao déficit de irrigação

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ABSTRACT - Due to the amount of water used in the agricultural sector, compared to other activities, irrigation must be done carefully and based on knowledge of plant water relations. The aim of this work was to evaluate the physiological behavior of young black pepper plants (*Piper nigrum* L.), subjected to water deficit, as well as the potential for recovery after stress. In 5 L pots, the plants were subjected to different irrigation levels (100; 78; 58 and 32% of the control depth), with irrigation management performed by an automatic controller from a water tension sensor in the soil. The following traits were evaluated: leaf osmotic potential (Ψ_o), relative water content (RWC), stomatal conductance (*gs*) and photosynthetic pigments. To evaluate the plants' recovery capacity, substrate rehydration was performed when about 50% of the plants in a treatment had stomatal conductance (*gs*) close to zero. The different levels of water deficit reduced the values of all traits. In the treatment 32%, values of -2.39 MPa for Ψ_o, 60% for RWC and *gs* close to zero were observed on the 28 th day of water restriction. After three days of rehydration of this treatment, the recovery of these values was partial, not reaching the values of the treatments 100 and 78%. Black pepper plants showed high susceptibility to water restrictions and low capacity for recovery after stress.

Key words: Osmotic potential. Stomata. Stomatal conductance. Water stress.

RESUMO - Em razão da quantidade de água utilizada no setor agropecuário, comparada às outras atividades, a irrigação deve ser feita de forma criteriosa e com base no conhecimento das relações hídricas vegetais. O objetivo deste trabalho foi avaliar o comportamento fisiológico de plantas jovens de pimenta-do-reino (*Piper nigrum* L.), submetidas a restrições hídricas, assim como o potencial de recuperação após o estresse. As plantas, cultivadas em potes de 5 L, foram submetidas a diferentes níveis de irrigação (100; 78; 58 e 32% da lâmina controle), com manejo realizado por acionamento automático a partir de um sensor de tensão da água no solo. Foram avaliados: potencial osmótico foliar (Ψ_o), conteúdo relativo de água (CRA), condutância estomática (*gs*) e pigmentos fotossintéticos. Para avaliar a capacidade de recuperação das plantas, houve reidratação do substrato quando cerca de 50% das plantas de um tratamento apresentassem condutância estomática (*gs*) próxima a zero. Os diferentes níveis de déficit hídrico reduziram os valores de todas as variáveis. No tratamento 32% foram observados valores de -2,39 MPa para Ψ_o, 60% para CRA e *gs* próxima a zero no 28º dia de restrição hídrica. Após três dias de reidratação deste tratamento, a recuperação desses valores foi parcial, não atingindo os valores dos tratamentos 100 e 78%. Plantas de pimenta do reino exibiram elevada susceptibilidade a restrições hídricas e baixa capacidade de recuperação após estresse.

Palavras-chave: Potencial osmótico. Estômatos. Condutância estomática. Estresse hídrico.

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INTRODUCTION

Black pepper (*Piper nigrum* L.), also known in Brazil as 'pimenta-do-reino', is a species belonging to the *Piperaceae* family and adapted to tropical and subtropical climate, having the south of India as its region of origin. It is currently widely cultivated in countries such as Vietnam, Malaysia and Indonesia. In Brazil, the states of Pará and Espírito Santo are the largest producers, with 22.75 and 21.48 thousand tons produced in 2017, respectively, representing about 94% of the total produced in the country (INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA, 2018).

In the Northeast region of the state of Espírito Santo, due to the long periods of drought, water deficit becomes the main limiting factor for production. Water is an indispensable element for plant growth and yield, and if its supply is limited, some morphological, physiological and biochemical attributes of the plant can be compromised (IQBAL *et al*., 2018). Among the abiotic factors, drought is the greatest limiting factor for the yield of several crops, being frequently related to changes in cell volumes and as a consequence with the loss of turgor, interruption of water potential gradients and limitations to the diffusion of gases (KAVROULAKIS *et al*., 2018).

Some studies indicate that different varieties of the same species may express physiological or morphological differences when subjected to water deficit. Some drought-tolerant species have developed mechanisms such as deeper root systems, control of stomatal closure and reduction of leaf area, maximizing the use of water for biomass production (PINHEIRO *et al*., 2005). According to Tonello and Teixeira Filho (2013), plants that grow under moderate water stress conditions or even under drought conditions modify their stomatal conductance during different periods of the day, in addition to reducing the water potential of the leaf, leading to the loss of turgor and stomatal closure.

The occurrence of environmental stresses represents a threat to food production and, therefore, it is necessary to develop technologies to produce more efficiently and with saving natural resources, in view of the growing demand for food, caused by the increase in the world population, which is estimated to reach 8.9 billion by 2050 (KUMAR; VERMA, 2018).

Studies conducted by Krishnamurthy *et al*. (2016) in India show that black pepper plants in reproductive stage have water need from 2,000 to 3,000 mm, being a crop sensitive to water deficit. However, there are few studies on its physiological behavior under drought conditions. In view of the above, the objective of this study was to evaluate the physiological conditions in young black pepper plants subjected to different irrigation levels and their capacity for recovery after being subjected to water deficit.

MATERIAL AND METHODS

The experiment was carried out in a greenhouse in the Horticulture Sector of the Plant Science Department of the Federal Rural University of Rio de Janeiro (UFRRJ), located in the municipality of Seropédica - RJ, Brazil (22º 45' 48" South and 43º 41' 50" West), in November and December 2018.

The experiment was conducted using young black pepper plants *cv*. Bragantina, 180 days old, produced from cuttings with two nodes in a commercial nursery located in São Mateus - ES. For acclimatization, shortly after arrival at the experiment site, the seedlings remained for 15 days in a greenhouse with automatic control of temperature (not exceeding 30 °C) and relative humidity (not less than 60%). After this period, they were transferred to a greenhouse without temperature and relative humidity control and transplanted to 5.0-L plastic pots, which were filled with soil from the surface layer of a *Planossolo* (Alfisol) (OLIVEIRA *et al*., 2018), so that the average packaging density was 1.58 g cm^{-3}. Chemical analysis of the soil showed the following characteristics: pH = 6.2; Na^+ = 0.13 cmolc dm^{-3}; Ca^{2+} = 4.5 cmolc dm^{-3}; Mg^{2+} = 1.9 cmolc dm^{-3}; K^+ = 83 mg dm^{-3}; P = 122 mg dm^{-3}.

During the first 10 days after transplanting, the plants were subjected to rustification (previous imposition of unfavorable conditions for better adaptation in the field) and acclimatization processes, being irrigated with 100% of the reference depth (control). At the end of this period, the initial moisture of the substrates was standardized, initiating the application of irrigation levels (IL). The experimental design used was completely randomized, in a unifactorial scheme, with eight repetitions. ILs consisted of the application of 100 (IL100), 78 (IL78), 52 (IL52) and 32% (IL32) of the control depth.

The irrigation system was supplied by a motor pump set, automatically activated by the automatic actuator for irrigation (AAI) (MEDICI *et al*., 2010; MELLO *et al*., 2018). The height difference between the center of the porous cup (sensor) and the pressure switch was 0.4 m, indicating an irrigation management with maintenance of the water tension in the substrate around 4.0 kPa.

The different irrigation depths were applied using Netafim drippers (mod. PCJ-HCNL) with nominal flow rates of 4.0, 3.0, 2.0 and 1.2 L h^{-1}, subjected to pressure of 50 kPa. The porous cup of the AAI was installed in an irrigated plot containing the dripper with the highest flow rate (control). Emitter flow tests were performed and indicated distribution uniformity coefficient (DUC) above 95% in all treatments.

The amount of water applied was monitored by means of periodic readings in a water flow meter (model Alpha mnf/Fae Technology Company - Fortaleza/CE) installed in the main line of irrigation. Weather conditions were monitored by the automatic station WatchDog (Spectrum Technologies, Inc. – Aurora, IL/USA) installed inside the greenhouse, programmed to store the data every five minutes. From air temperature and relative humidity, the saturation vapor pressure and the partial vapor pressure were estimated and then used to calculate the vapor pressure deficit (VPD). The highest temperatures were recorded in the period from 29 to 33 days of water restriction (DWR), with a maximum of 43 ºC, higher than the range considered ideal for the black pepper crop, which is 23 to 32 ºC according to Krishnamurthy *et al*. (2016), with no tolerance to temperatures above 40 ºC. Periods with mild temperatures and high relative humidity, resulting in low VPD, were verified between days 14 and 16 DWR, and 24 and 26 DWR.

The evaluations of stomatal conductance (*gs*), chlorophyll indices, leaf osmotic potential (Ψ_o) and relative water content (RWC) were always performed in young and fully expanded leaves, preferably exposed to solar radiation. A porometer (SC-1 Leaf Porometer, METER Group, Inc. – Pullman, WA/USA), a chlorophyll meter (ClorofiLOG CFL1030, Falker Automação Agrícola – Porto Alegre/RS) and the WP4C potential meter (METER Group, Inc. – Pullman, WA/USA) were used. Readings of Ψ_o and RWC were performed from 12:00 to 14:00 h; chlorophyll from 09:00 to 11:00 h; porometry from 09:00 to 10:00 h (morning) and from 13:00 to 14:00 h (afternoon). Before each evaluation, the substrate moisture was determined by weighing each experimental plot on a balance, with 30.0 kg capacity and 0.5 g accuracy. During the evaluations, the automatic actuator was turned off, so that irrigation would not occur in these periods, and the weather station was reprogrammed to record data every minute.

Readings of chlorophyll indices (*a*, *b* and total) and *gs* were performed at 0, 9, 15, 22, 23, 27, 28, 29, 30, 31, 32 and 33 DWR. Due to excess cloudiness, it was not possible to perform morning readings at 28 and 29 DWR. At 23, 28 and 31 DWR, Ψ_o readings and RWC determination were performed. For the determination of Ψ_o, a sample was collected in the youngest fully expanded leaf of each plant, provided that it was free of damage and had its greatest width above 40 mm (diameter of the circular samples collected). After collection, the samples were placed in containers that are specific for readings in WP4, identified, stored in thermal box and transported to the laboratory. The samples remained at a temperature of approximately -10 °C in a refrigerator until the day after collection, when the Ψ_o readings were performed.

In the same leaves used for Ψ_o evaluation, five discs with 6.0 mm diameter each were collected using an adapted paper puncher. The discs were immediately placed in containers with lid and sealed, in order to avoid significant water loss. Then, they were properly identified and transported to the laboratory, where each disc was weighed on a semi-analytical scale, making it possible to obtain fresh mass (FM). Subsequently, the discs were immersed in deionized water and remained for 24 hours. Soon after, the discs were removed, dried on paper towels and weighed again, to determine the turgid fresh mass (TFM). Then, the discs were dried in a forced circulation oven at 60 °C for 72 h or until reaching constant mass, making it possible to obtain the values of dry mass (DM). The RWC values, in percentage, were obtained using equation 1 (CIA *et al*., 2012).

$$RWC = \frac{FM - DM}{TFM - DM} \times 100 \qquad (1)$$

At 28 DWR, it was observed that at least 50% of the plants in the IL32 treatment showed *gs* tending to 0.0 mmol m^2 s^{-1}. For this reason, the moisture of the substrates of these plants was increased to the container capacity, and the plants began to receive water in volumes identical to those applied to the control treatment (IL100), until the end of the experiment.

All statistical analyses were carried out in the statistical package R, version 3.6.0. To meet the assumptions of statistical analysis, the normality and homogeneity of the residuals were verified, respectively, by the Shapiro-Wilk and Bartlett tests, at 5% probability level. There was no need to transform the data to meet the assumptions. When a significant difference was found between the treatments, the data were subjected to regression analysis.

RESULTS AND DISCUSSION

The average volumes of water applied up to the moment of rehydration of the IL32 treatment (28 DWR) were 2.81, 2.19, 1.46 and 0.90 L per plant for IL100, IL78, IL52 and IL32, respectively. In the period from 28 to 33 DWR, the volumes applied were 0.96, 0.75, 0.50 and 0.96 L per plant, respectively. The period of highest water demand and highest frequency of actuation of the irrigation system occurred between 27 and 33 DWR, when about 39% of the total volume was applied for the IL100 treatment (Figure 1). This result may be related to the occurrence of higher VPD values and the abrupt drop in relative humidity.

Ψ_o was significantly affected by the different irrigation levels applied. At 23 DWR, values of -0.80 and -1.44 MPa were verified, respectively, in plants under full irrigation (IL100) and under maximum water restriction (IL32) (Figure 2). At 28 DWR, when the lowest substrate moisture occurred for IL32 (0.08 $cm^3 cm^{-3}$), there was a significant reduction in the Ψ_o of the plants, reaching -2.69 MPa.

A reduction of Ψ_o was also observed in the other treatments, including in the one which received 100% of the irrigation depth, where the Ψ_o was equal to -1.00 MPa. This reduction may have been caused by the VPD value when the material was collected (4.6 kPa), which is higher than that estimated in the previous collection (2.7 kPa). This variation of VPD was caused by the temperature and relative humidity at the time of collection of the leaves, which were 32.8 ºC and 46.2% at 23 DWR and 38.4 ºC and 32.2% at 28 DWR, respectively.

On the third day after rehydration, the Ψ_o values were not described by any regression model. In this period, plants that were previously subjected to the most severe restriction had lower values of Ψ_o (-1.18 MPa), while in fully irrigated plants, the Ψ_o in the same period was 44% higher (-0.79 MPa). Rivas *et al*. (2016) report that the water potential in cowpea reached its minimum value at 10 days of water stress (-1.5 MPa), showing total recovery after 5 days of rehydration. Leaf water potential in cupuaçu plants showed total recovery on the third day of rehydration (CUNHA *et al*., 2018), due to the ability of this species to perform osmotic adjustment.

The values of Ψ_o verified at 28 DWR (Figure 2), associated with low values of RWC in the same period (Figure 3), indicate that black pepper plants do not perform osmotic adjustment as a form of protection against excessive dehydration, when subjected to environments with low water availability. However, studies on the accumulation of intracellular substances that confirm this behavior are necessary.

Plants that perform osmotic adjustment have the ability to accumulate a series of inorganic compounds (Na^+, K^+, Cl^-) and/or organic compounds (proline, soluble sugar, glycine betaine) that contribute to the osmotic adjustment of their cells (BLUM, 2017). In black-eyed pea crop under water stress conditions, Merwad, Desoky and Rady (2018) observed that the osmotic adjustment favored the growth and development of plants.

At 23 DWR, a reduction in RWC was observed as the restriction of the applied water level increases (Figure 3). Higher estimated values of RWC were verified in IL100 and IL78 treatments, remaining at 97.5 and 85.6%, respectively, while IL52 and IL32 showed estimated RWC values of 71.6 and 60.7%, respectively. According to Cockerham and Leinauer (2011), well-hydrated plants generally remain with RWC values between 85 and 95%. At 28 DWR, RWC reduction was observed in all treatments in relation to the 23 DWR. During this period, the respective RWC values for IL100, IL78, IL52

Figure 1 - Volume of water supplied to black pepper plants (*cv*. Bragantina) in each treatment during water restriction days (11/13/2018 to 12/16/2018)

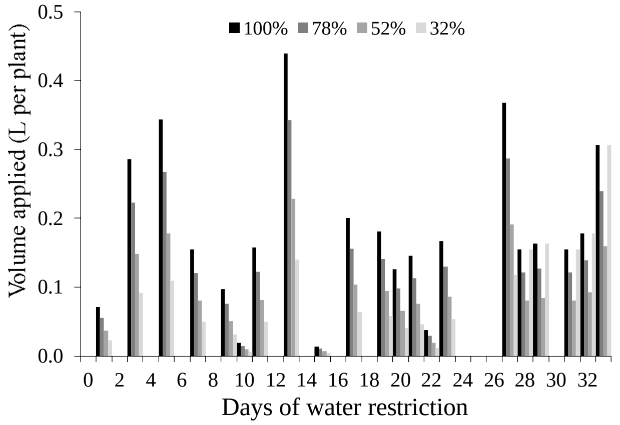


Figure 2 - Osmotic potential (Ψ_o) in the leaves of black pepper (*cv*. Bragantina) at 23, 28 and 31 days of water restriction (DWR), as a function of irrigation levels

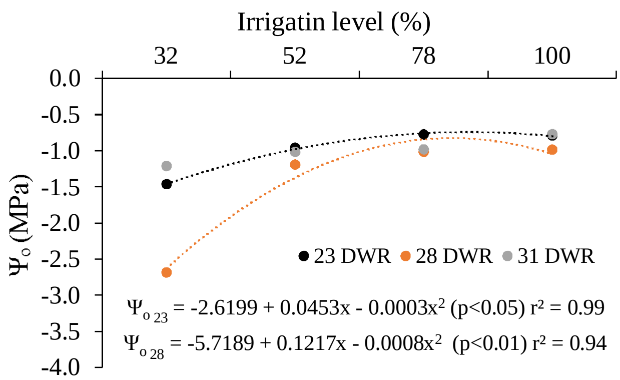
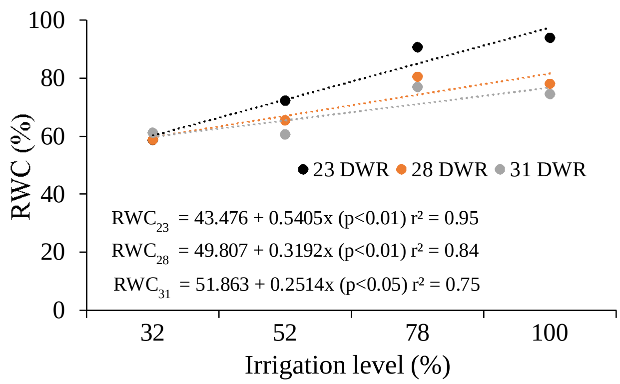


Figure 3 – Relative water content (RWC) in seedlings of black pepper (*cv*. Bragantina) at 23, 28 and 31 days of water restriction (DWR), as a function of irrigation levels



and IL32 treatments were 81.7, 74.7, 66.4 and 59.7% (Figure 3), and in the last mentioned treatment the plants had *gs* values close to zero.

The reductions of RWC in treatments with higher water deficit can be explained by the lower availability of water in the soil, associated with higher atmospheric demand. However, the reduction of RWC values for the fully irrigated treatment may have been affected by the higher rate of stomatal opening, resulting in higher water losses to the atmosphere and favoring momentary dehydration of leaves. In soybean crop, leaf water potential and conductance are influenced by the change in climatic conditions throughout the day, being lower in times of higher VPD (LOCKE; ORT, 2015).

At 31 DWR, the RWC values for the IL100 and IL78 treatments did not show considerable variations compared to the previous evaluation. In this period, plants that received 52% of the maximum irrigation had RWC of 65%, while in the rehydrated treatment, RWC values were close to 60% on the third day of rehydration. It is worth pointing out that in the period of RWC and osmotic potential readings, at 31 DWR, climatic conditions were the most unfavorable. The momentary VPD reached 5.6 kPa, for a temperature of 40.7 °C and relative humidity of 26.7%.

Evaluating two varieties of cowpea subjected to water stress, Rivas *et al*. (2016) verified that the water potential in the leaves showed total recovery, being similar to the non-irrigated treatment, after two days and rehydration.

At the beginning of the experiment (0 DWR), when the substrate moisture conditions were similar for all treatments, the values of *gs* ranged from 171.6 to 231.2 mmol m^2 s^{-1} in the morning and from 172.8 to 221.6 mmol m^2 s^{-1} in the afternoon, with no fit of models to the data series (Figure 4A). Between 9 and 28 DWR, the values of *gs* were significantly influenced by the irrigation levels applied, being higher in plants that received 100% of irrigation, due to the higher availability of water in the soil and, consequently, the higher rate of stomatal opening. The results corroborate those of Akhtar *et al.* (2014) and Gavilli, Moosavi and Haghighi (2019), who evaluated tomato and soybean plants, respectively, and found a reduction of *gs* when deficit irrigation was applied. In this period, the values of *gs* in the morning were usually higher than those measured in the afternoon, showing that stomatal closure occurs partially in plants with lower irrigation level, being considered a plant defense mechanism to avoid water deficit (YANG *et al*., 2018) (Figure 4).

The *gs* rates at 28 DWR indicate that plants subjected to the highest water restriction (IL32) showed total closure of stomata at the hottest times of the day, while in plants under full irrigation, *gs* was equal to 116.7 mmol m^2 s^{-1} (Figure 4G). According to Gadi *et al*. (2019), large water losses through the stomata associated with the lower amount of available water can cause damage to the guard cells, resulting in low values of stomatal conductance. The low value of *gs* found in the IL32 treatment on its last day of stress (28 DWR), associated with the low RWC, shows that stomatal closure occurred when leaf cells had low water content and, thus, low cell turgor.

One day after rehydration of the treatment that had received 32% of the total volume of water, *gs* reached 57 mmol m^2 s^{-1} in the afternoon, while in the same period the treatments IL52 and IL78 showed values of 77 and 104 mmol m^2 s^{-1}, respectively, and these were maintained in their respective values of water restriction (Figure 5A).

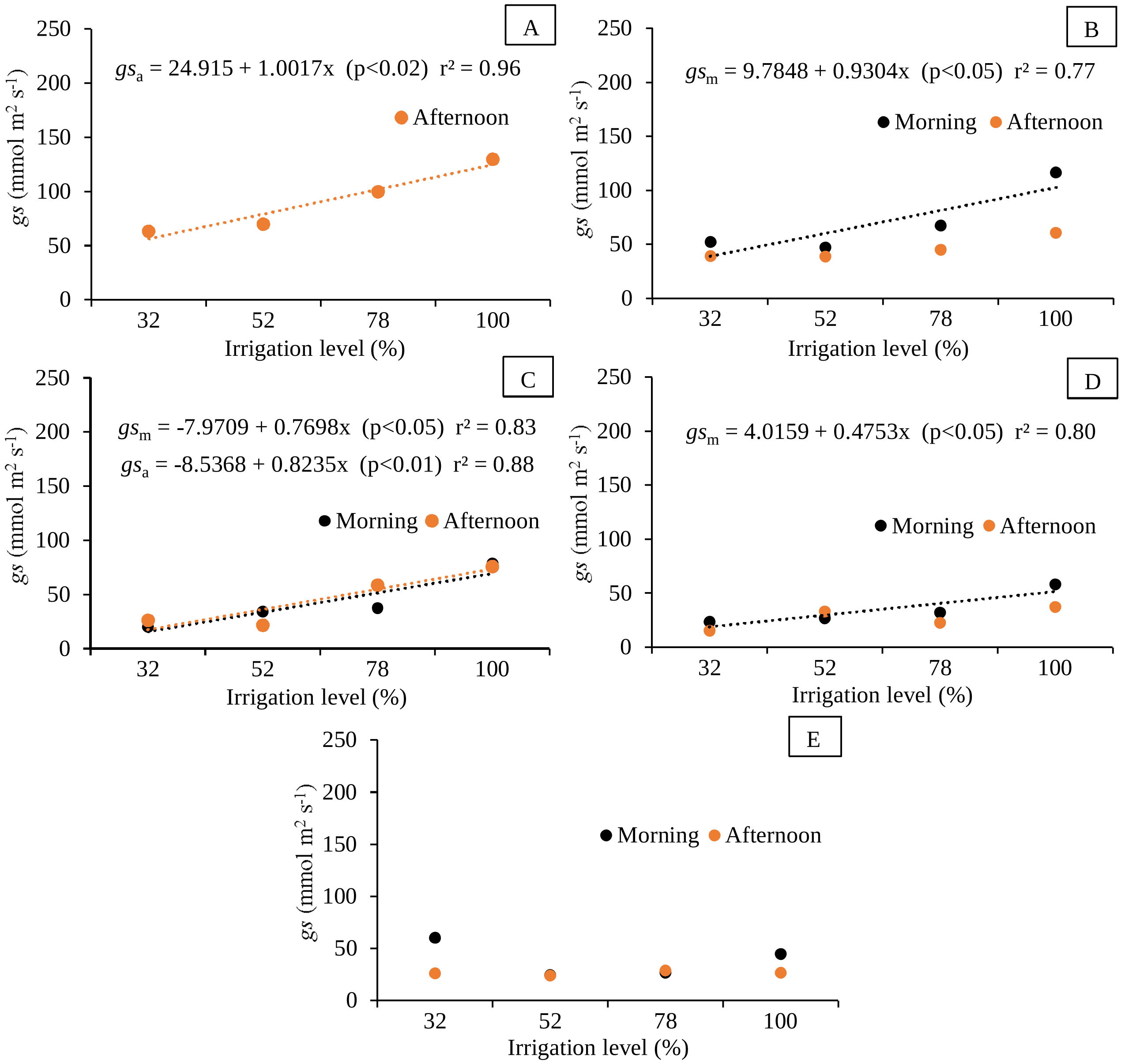
The increase in *gs* after the elevation of soil moisture occurred due to the greater stomatal opening. A trend similar to that found at 29 DWR was observed at 30 DWR, with a slight increase in *gs* in the rehydrated treatment and higher rates of *gs* in the IL100 and IL78 treatments in the morning (Figure 5B). In the afternoon, the values of *gs* in all treatments did not vary significantly, being 102.8, 82.4, 58.2 and 39.6 mmol m^2 s^{-1} for IL100, IL78, IL52 and IL32, respectively. This is due to the increase in VPD that occurred on the day, and the afternoon analysis was performed at times of higher temperatures.

At 31 (Figure 5C) and 32 DWR (Figure 5D), very similar values of *gs* were observed during the morning and afternoon periods. The treatment with full irrigation (IL100) showed a reduction in stomatal opening when compared to the previous days, as it was the hottest and driest period of the experimental period. Stomatal closure in fully irrigated plants is due to increased water loss by the leaves and the inability of roots to absorb water in sufficient quantity to meet the demand of the shoots (KAVROULAKIS *et al*., 2018).

At 33 DWR, the *gs* values were not described by any regression model due to the low variance between treatments (Figure 5E). However, it is observed that, in the morning, maximum *gs* values were observed in the rehydrated treatment (60 mmol m^2 s^{-1}), while the values in the treatments IL100, IL78 and IL52 were equal to 44.7, 26.8 and 24.3 60 mmol m^2 s^{-1}, respectively. These results corroborate those of Ghannoum (2009), who verified photosynthetic recovery after rehydration of the plants. Plants with higher photosynthetic rates, and consequently higher CO_2 consumption, also have higher values of *gs* (SANTOS *et al*., 2018). Therefore, the *gs* values tended to recover after only five days of rehydration.

Variations were observed in the chlorophyll *a*, chlorophyll *b* and total chlorophyll indices of black pepper

Figure 4 - Stomatal conductance (*gs*) in seedlings of black pepper (*cv.* Bragantina) on different days of water restriction (DWR) and in the morning (m) and afternoon (a) as a function of irrigation levels. (A) 0 DWR. (B) 9 DWR. (C) 15 DWR. (D) 22 DWR. (E) 23* DWR. (F) 27 DWR. (G) 28** DWR. **gs* estimated only in the afternoon.**gs estimated only in the morning



plants subjected to water deficit (Figure 6). Initially, only reduction in pigment contents was observed in the period from 0 to 15 DWR, occurring similarly for all treatments, probably due to the process of rustification of plants to the environment without temperature and relative humidity control, although they remained for 10 days in this process before the treatments with water deficit started.

Higher chlorophyll *a* indices were verified in the fully irrigated treatment, ranging from 40.5 (15 DWR) to 39.0 FCI (32 DWR) (Figure 6A). The treatments IL52 and IL32 showed the highest variations of chlorophyll *a*, respectively ranging from 38.4 and 40.0 to 20.9 and 21.8 FCI in the period from 15 to 32 DWR. Similar behavior occurred for chlorophyll *b* content, with the highest levels measured in the fully irrigated treatment, ranging from 18.5 (15 DWR) to 13.6 FCI (32 DWR) (Figure 6B). Similarly, the greatest variations were observed in the treatments IL52 (17.2 to 8.6 FCI) and IL32 (11.6 to 6.1 FCI).

The reduction of chlorophyll content with increasing water deficit is mainly due to the formation of reactive oxygen species, such as O_2 and H_2O_2, which can lead to lipid peroxidation and, consequently, chlorophyll degradation (SHIVAKRISHNA; REDDY; RAO, 2018).

Figure 5 - Stomatal conductance (*gs*) in seedlings of black pepper (*cv*. Bragantina) on different days of water restriction (DWR) and in the morning (m) and afternoon (a) as a function of irrigation levels. (A) 29* DWR. (B) 30 DWR. (C) 31 DWR. (D) 32 DWR (E) 33 DWR. **gs* estimated only in the afternoon

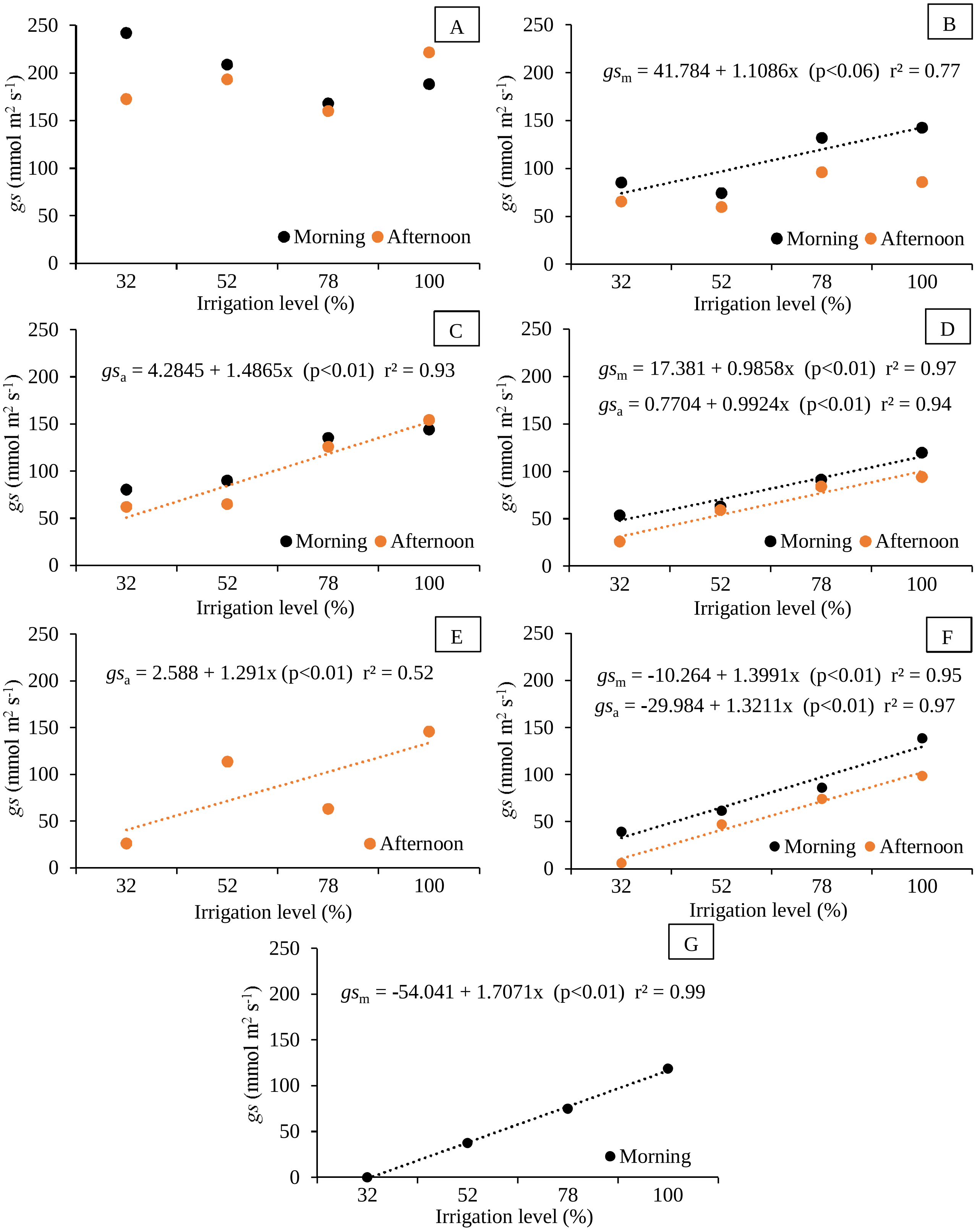
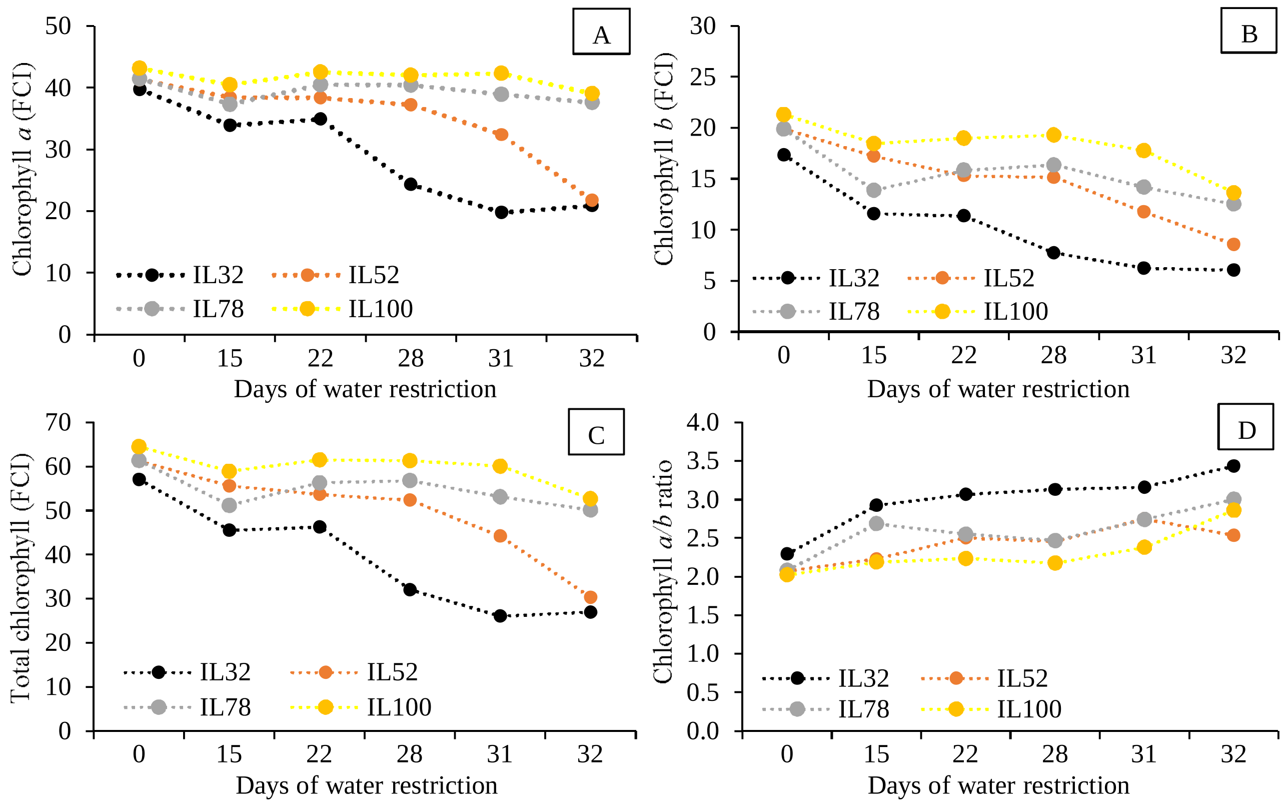


Figure 6 - Chlorophyll indices and chlorophyll *a*/*b* ratio in seedlings of black pepper (*cv*. Bragantina) along the experimental period. (A) Chlorophyll *a*. (B) Chlorophyll *b*. (C) Total chlorophyll. (D) Chlorophyll *a*/*b* ratio



The oscillation in the values of total chlorophyll content followed a behavior similar to that observed for chlorophylls *a* and *b* along the evaluation period (Figure 6C). There was a variation of 11% for the fully irrigated treatment in the period from 15 to 32 DWR; for the treatments IL78, IL52 and IL32, the variations were 2, 46 and 41%, respectively, with the lowest percentage of variation in the IL78 treatment.

Studying four different genotypes of quinoa, Iqbal *et al*. (2018) found higher contents of chlorophylls *a* and *b* and carotenoids in irrigated plants and lower contents of these pigments in plants subjected to drought. According to the authors, plants subjected to drought suffer greater oxidative damage. After 28 DWR, there was a reduction in the total contents of photosynthetic pigments, due to the period of high solar irradiation and high temperatures, which can cause damage to leaf pigments. A possible explanation for the stability in the total chlorophyll content of the IL78 treatment is the trend of reduction in leaf growth, which causes an effect of concentration of the pigments under mild drought, as reported by Valença *et al*. (2018).

The most severe water stress caused an increase in the chlorophyll *a*/*b* ratio (Figure 6D). This may be associated with a decrease in the size of the light-harvesting antenna of photosystem II (PSII), due to the lower electron transport between the photosystems (KITAJIMA; HOGAN, 2003). According to Liu *et al*. (2011), the increase of the chlorophyll *a*/*b* ratio in plants subjected to water stress can be explained as a decrease in peripheral light-harvesting complexes. Similar results were observed by Guo *et al*. (2016) in seedlings of *Lycium ruthenicum* Murr. under drought and by Maia Júnior *et al*. (2019) in sugarcane cultivars under severe drought.

At the end of the experiment, it was possible to observe the death of plants, regardless of the treatment applied, caused by the high temperatures recorded from 25 DWR. Temperatures above 40 ºC and high VPD values worsened plant survival conditions, resulting in large water losses to the atmosphere. According to Krishnamurthy *et al*. (2016), the maximum air temperature tolerated by this crop is 40 ºC, and the ideal range for soil temperature is 26-28 ºC, for the development of the roots to be satisfactory.

In view of the above, it is necessary to conduct studies evaluating the effect of thermal stress on black pepper plants, thus verifying whether high temperatures associated with low air humidity inhibit their development or whether the development is possible when these plants are subjected to high temperatures and high relative humidity.

CONCLUSIONS

1. The effect of water deficit caused a reduction in stomatal conductance, Ψ_o and RWC in the leaves of black pepper plants. Three days of recovery after water restriction are not sufficient for these variables to show values similar to those found in the control with full irrigation;
2. Black pepper plants fully irrigated with AAI show physiological behavior that indicates better capacity to develop. However, even fully irrigated plants do not withstand temperatures above 40 ºC associated with low relative air humidity.

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