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CROP PRODUCTION

Morphophysiological changes in black pepper under different water supplies

Gean Corrêa Teles[1], Leonardo Oliveira Medici[2], David da Cunha Valença[3], Eleandro Silva da Cruz[4] and Daniel Fonseca de Carvalho[5*]

[1]Programa de Pós-graduação em Fitotecnia, Instituto de Agronomia, Universidade Federal Rural do Rio de Janeiro, BR-465, km 7, 23897-000, Seropédica, Rio de Janeiro, Brazil. [2]Departamento de Ciências Biológicas, Instituto de Ciências Biológicas e da Saúde, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil. [3]Departamento de Botânica, Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro, Rio de Janeiro, Brazil. [4]Instituto Nacional de Colonização e Reforma Agrária, Vila Velha, Espírito Santo, Brazil. [5]Departamento de Engenharia, Instituto de Tecnologia, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil. *Author for correspondence. E-mail: daniel.fonseca.carvalho@gmail.com

ABSTRACT. The center of origin and domestication of *Piper nigrum* L. are in high rainfall regions. But when grown in regions with irregular or insufficient rainfall, irrigation becomes essential. This study evaluated the impact of irrigation levels on the physiological and growth characteristics of black pepper plants, cv. Bragantina. It was carried out from April 2019 to May 2020, using automatic activation irrigation. We used emitters with different flow rates to apply water depths corresponding to 100, 81, 62, and 42% of the crop water requirement. The parameters evaluated comprised main stem length (MSL), stem diameter (SD), number of leaves (NL), leaf area (LA), chlorophyll contents, chlorophyll-*a* fluorescence, and some photosynthetic parameters. The treatments significantly influenced ($p < 0.05$, F-test) MSL and NL. Plants submitted to the control treatment showed MSL (65.8%) and NL (123%) greater than those irrigated with the smallest volume ($p < 0.05$, F-test). However, the treatments had no significant effect on SD. Moreover, chlorophyll *b* levels decreased by 26% and chlorophyll *a*/*b* ratio increased by 22% at 120 and 180 DAT, respectively. Some photosynthetic parameters such as FV/FM, ABS/RC, and DI0/RC were affected by water deficit at 120 DAT. Our results suggest the sensitivity of black peppers to water deficit and contribute to the proper management of this crop.

Keywords: *Piper nigrum* L.; chlorophyll *a* fluorescence; water deficit; simplified irrigation controller.

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Introduction

Reducing water waste in irrigation is one of the challenges for agriculture, which corresponds to about 70% of global water demand and plays a key role in global food security (FAO, 2020). In this context, proper irrigation management makes it possible to meet crop water requirements, avoiding production losses due to water deficit or nutrient leaching due to excess water.

Black pepper (*Piper nigrum* L.) is the most consumed spice worldwide and economically valued product with good acceptance in the foreign market (Tran et al., 2019). The Brazilian production of black pepper is among the five largest ones (FAOStat), and about 95% of it is concentrated in the states of Pará and Espírito Santo (IBGE, 2020). In addition to seasonings and condiments, *Piper nigrum* L. fruits are also used for the extraction of piperine, which is an active ingredient used in the pharmaceutical industry due to its therapeutic properties (Gorgani, Mohammadi, Najafpour, & Nikzad, 2017; Shityakov et al., 2019). However, although it is cultivated globally, especially in tropical climate regions, its water demands have been little studied. Such information is highly relevant in regions with poorly distributed or below-demand rainfall volumes given its water deficit sensitivity (Rasanjali, Silva, & Priyadarshani, 2019; Gorgani et al., 2017).

The sensitivity of black peppers to water deficit increases their need for continuous water supply (Raj, 1978). In this context, the fine adjustment of soil water tension promoted by the Simplified Irrigation Controller (SIC) (Mello et al., 2018) has shown some efficiency in saving water for crops in the field or a protected environment. Similarly, the use of different irrigation volumes through SIC can help achieve higher soil water tensions, besides enabling the physiological study of plants at a variable irrigation rate (Valença et al., 2018).

Vegetative growth and physiological parameters associated with drought may indicate tolerance to water deficit in plants and serve as stress indicators, which can help in decision making (Rong-hua, Guo, Michael, Stefania, & Salvatore, 2006). For photosynthesis, under water deficit, there is a limitation of CO_2 diffusion to Rubisco carboxylation sites, which may compromise biochemical and photochemical phases due to stomatal closure. Chlorophyll-*a* fluorescence measurements provide drought indicator parameters, which can demonstrate damages of varying magnitudes in photosynthetic apparatus. Similarly, chlorophyll content can also be an indicator of plant stress by water deficit. In this case, losses in chlorophyll *a* and *b* content by oxidative processes have negative effects on photosynthetic efficiency when under severe droughts (Van Der Mescht, De Ronde, & Rossouw, 1999). Conversely, under mild drought, these pigments may accumulate because of lower plant growth rates (Valença et al., 2018).

In this study, fresh and dry masses, number of leaves, chlorophyll a fluorescence, and chlorophyll a and b contents were evaluated in black pepper plants subjected to different irrigation volumes managed through the SIC. Moreover, vegetative growth parameters were related to the number of degree-days accumulated throughout the experiment. All these data can serve to characterize this species in terms of water deficit, thus helping irrigation management to save water.

Material and methods

The study was conducted in the state of Rio de Janeiro (southeastern Brazil) (22°45'48.5" S 43°41'51.2" W, 33-m altitude) in cultivation pots kept in the open field. According to Köppen's classification, the local climate is an *Aw* type, which stands for rainy summers and well-defined dry winters, with July being the driest month.

At 120 days after planting of cuttings, black pepper seedlings (cv. Bragantina) were transplanted into 25-L flexible plastic packages, maintaining one seedling per pot. The pots were filled with substrate composed of soil from the A horizon of a *Planossolo* (Alfisol) (60% clay, 30% sand, and 10% silt), whose chemical characteristics were: pH (in water) 5.3; 56 mg dm^{-3} phosphorus; 63 mg dm^{-3} potassium; 2.7 $cmol_c$ dm^{-3} calcium; 1.2 $cmol_c$ dm^{-3} magnesium; 0.1 $cmol_c$ dm^{-3} aluminum; and 0.09 $cmol_c$ dm^{-3} sodium.

The substrate was fertilized following the recommendation for the crop of the Manual of Recommendation of Liming and Fertilization for the state of Espírito Santo (Prezotti, Gomes, Dadalto, & Oliveira, 2007). Nitrogen (N) and potassium (K) doses were split into three applications (at 30, 60, and 90 days after transplantation - DAT), while phosphorus (P) dose was applied all at once at the time of transplantation.

Experimental design and irrigation system

The experimental design used was randomized blocks (RBD), with four treatments and six blocks. Each experimental plot consisted of two plants, one in each pot. The pots were spaced 1.0 m apart within rows and 1.5 m apart between rows. The treatments consisted of water application via a drip irrigation system, combining different pressure-compensating emitters, PCJ model (Netafim Brasil, Ribeirão Preto, São Paulo State), resulting in flow rates of 2.2 (V1), 3.3 (V2), 4.3 (V3), and 5.3 (V4) L h^{-1}. Flow rate tests were performed in the field and indicated water distribution uniformity coefficients above 95% for all treatments.

Irrigation was managed using two simplified irrigation controllers (SIC) (Mello et al., 2018), which were installed in two distinct blocks, in experimental plots that received the highest flow rate treatment (V4). As this flow rate provided enough water to meet crop water requirements, V4 was considered a control treatment. The SICs, which operate based on tensiometry, were composed of a ceramic candle, just as those used in residential filters, connected by a transparent hose to a pressure switch. The ceramic candles were installed at 15 cm depth from the substrate surface and, 40 cm below them, pressure switches were installed to allow irrigation system to be activated automatically when the water tension in control substrate reached 4.0 kPa. This tension has often been used in automatic irrigation systems for forest tree species (Bueno, Leles, Abreu, Santos, & Carvalho, 2020; Bueno et al., 2021), black pepper seedlings (Cruz et al., 2022), ornamental plants (Santos, Pego, Couto, Bueno, & Carvalho, 2020; Martins, Pego, Cruz, Abreu, & Carvalho, 2021), among others. Therefore, irrigation was actuated simultaneously in all pots, but at volumes varying according to the emitter flow rates (V1, V2, V3, and V4).

Weather monitoring

Data obtained from the weather station of the INMET (Agricultural Ecology - A601) located in the city of Seropédica was used to estimate effective rainfall depth (RDef), which was calculated by the curve number method proposed by the Soil Conservation Service (Carvalho, Domínguez, Oliveira Neto, Tarjuelo, & Martínez-Romero, 2014). Maximum (T_{max}) and minimum (T_{min}) temperatures were used to calculate the daily thermal sum for black pepper crop by the model of Ometto (1981). To do so, upper (TB) and lower (Tb) basal temperatures were 40 and 10°C, respectively (Krishnamurthy, Ankegowda, Umadevi, & George, 2016).

Total water supply was calculated as volumes applied via irrigation system added to RDef values (converted into volume), considering a useful area of 0.0961 m^2 per pot.

Vegetative growth parameters

Every 15 days from transplantation to the end of the experiment, main stem length (MSL) was measured as the distance from the substrate surface to plant apex. Within the same interval, number of leaves (NL) and stem diameter (SD) were also determined, with the latter being measured between the first and second nodes above the substrate surface.

At the end of the experiment, at 392 DAT, leaf area (LA) was measured per plant using an LI-3100C leaf area integrator (LI-COR Biosciences, Lincoln/NE - USA).

Physiological parameters

Chlorophyll *a* (CHL_a) and *b* (CHL_b) indices were evaluated in two periods, initially every 15 days - from transplantation to 180 DAT - and from 345 to 390 DAT. In both periods, a CRL-1030 chlorophyll meter (Falker Automação Agrícola, Porto Alegre/RS) was used. Readings were performed on the youngest fully expanded leaves, preferably in a direction opposite to the sun. The total chlorophyll (CHL_{a+b}) and the ratio between CHL_a and CHL_b ($CHL_{a/b}$) were also considered as evaluation parameters. In this study, only results with significant differences were presented for a better discussion and understanding of the data.

Chlorophyll *a* fluorescence transient was measured at 120, 238, 386, and 391 DAT, using a portable fluorimeter (Handy-PEA, Hanstech, King's Lynn, Norfolk, UK). The measurements were performed at a time close to 11 am, sampling the youngest fully expanded leaves, which were adapted to the dark for 15 min. before reading. Fluorescence emission was induced with a pulse of saturating light (3 $mmol^{-2}$ s^{-1}) in a hole with a diameter of 4 mm for 1 s.

Measurements of initial (F_0), maximum (F_M), and variable ($F_V=F_M - F_0$) fluorescence were used to calculate the biophysical parameters of specific energy flows (ABS/RC, DIo/RC, TRo/RC, ETo/RC, and REo/RC), productivity (φ_{Po}, φ_{Eo}, and φ_{Ro}), quantum efficiency (Ψ_{Eo} and δ_{Ro}), and performance (PI_{abs} and PI_{Total}) established by the JIP test (Tsimilli-Michael, 2019; Tsimilli-Michael & Strasser, 2008).

Data analysis

For vegetative growth variables and chlorophyll indices, the normality and homogeneity of residuals were tested with the Shapiro-Wilk and Bartlett tests, respectively, at a 5% probability level. Afterwards, these data were subjected to ANOVA ($p = 0.05$) using the Sisvar software version 5.6 (Ferreira, 2019). When treatments were significantly different ($p < 0.05$), regression analyses were performed for MSL, SD, and NL as a function of the accumulated degree-days (ADD) and total volume of water applied, in this case including the variable LA, testing the linear and second-order polynomial models.

Regression models were analyzed by the least-squares method by matrix algebra (Ferreira, 2019). The most suitable regression models were selected considering the insignificance of regression deviation, the significance of model fit at 5% probability by the F-test, and higher coefficient of determination (R^2). Model identity equality (Graybill, 1976) were tested by F-test for fitted models referring to MSL, SD, and NL as a function of ADD to see if only one model was enough to explain variations in two or more treatments.

For chlorophyll indices at 120 and 180 DAT, when significance was observed by the F-test during ANOVA, the means were compared by the Tukey's test ($p = 0.05$).

Both the basic parameter F_V/F_M and biophysical parameters derived by the JIP test were compared relatively, through a radar chart, considering the plants subjected to treatment V4 as control.

Results and discussion

Vegetative growth parameters

The lowest irrigation volumes promoted reduced growth of main stem length (MSL), stem diameter (SD), and number of leaves (NL) throughout the experiment. All parameters increased linearly in response to accumulated degree-days (ADD). According to the identity test of models, only one model was enough to explain MSL variations over time for treatments V1 and V2 ($p > 0.05$, F-test), thus grouping these treatments. The same occurred for the response variable NL.

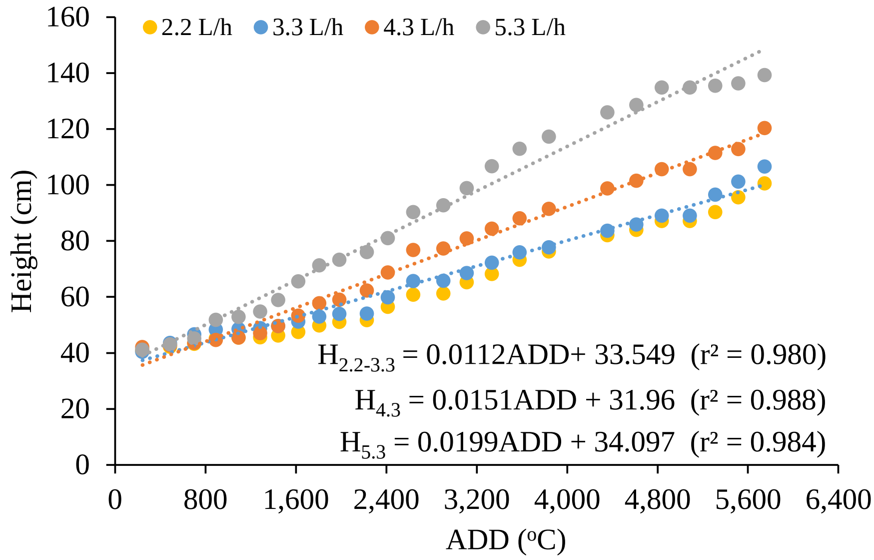

Figure 1. Main stem length changes of black pepper (cv. Bragantina) plants as a function of accumulated degree-days (ADD) (°C day) for each water volume applied.

From the beginning to the end of the experiment, MSL varied by about 62.5, 77.7, and 98.18 cm for treatments V1-V2, V3, and V4, respectively, differing by 65.8% between the lowest and highest irrigation levels applied. The plants reached, on average, 100 cm in MSL after 3,115, 4,614, and 5,740°C days when irrigated by V4, V3, and V2-V1, respectively. In a temporal analysis, these thermal levels were reached at about 224, 314, and 390 DAT, respectively (Figure 1).

At the end of the experiment, NL increased by 36.6, 60, and 81.8 leaves for treatments V1-V2, V3, and V4, respectively, varying by 123% from the highest to lowest irrigation volume. An average number of 40 leaves per plant was reached after 3,984, 2,199, and 1,857°C days in ascending order of the water volume applied (Figure 2).

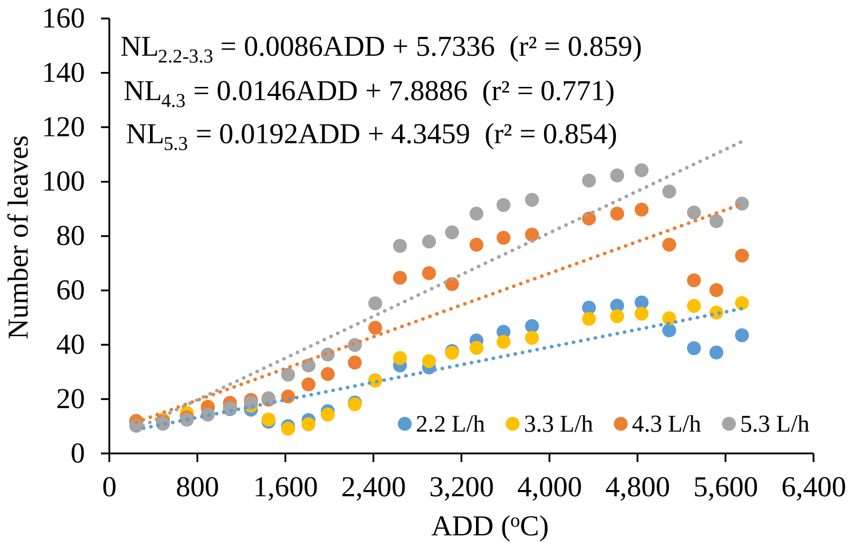

Figure 2. Increase in number of leaves (NL) as a function of accumulated degree-days (ADD) (°C day) in black peppers (*Piper nigrum*) subjected to different irrigation levels.

Averages of SD obtained were 8.64, 8.25, 8.85, and 9.51 mm for V1, V2, V3, and V4, respectively, showing increments of 82 and 88% at the lowest and highest irrigation levels, respectively. SD reached, on average, 8 mm after 3,115, 4,400, 4,400, and 4,800°C days when irrigated by V1, V2, V3, and V4, respectively (Figure 3).

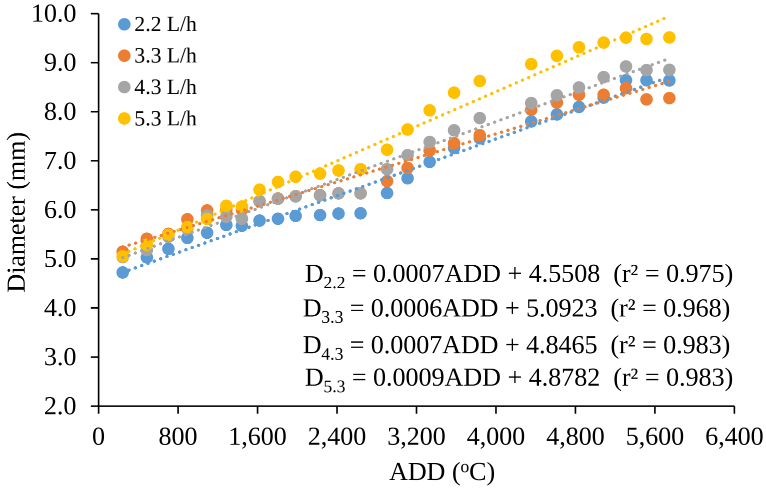

Figure 3. Stem diameter (mm) growth as a function of accumulated degree-days (ADD) (°C day) in black pepper (*Piper nigrum*) plants subjected to different irrigation levels.

As irrigation volume decreased plant growth decreased as seen in the evaluated morphological parameters. Larger irrigation volumes decreased the need for accumulated degree-days to promote gains in MSL, SD, and NL (Figures 1, 2, and 3). Radish plants also grew more with fewer degree days as the irrigation water level increased (Stagnari, Galieni, D'Egidio, Pagnani, & Pisante, 2018). Likewise, phenological cycle and accumulated degree-days varied in cotton subjected to different water stress levels (Zonta, Maniçoba, Brandão, Carrillo, & Bezerra, 2018).

Besides, other factors, this behavior can be explained by photoassimilate production reductions (Tatagiba, Pezzopane, & Reis, 2015) due to stomatal closure under water deficit conditions (Peloso, Tatagiba, & Amaral, 2017), limiting vegetative crop growth. This could be observed in various crops such as black pepper (*Piper nigrum*), bell pepper (*Capsicum annuum*), lilac (*Syringa oblata*), and euonymus (*Euonymus japonicus*) (Oliveira, Oliosi, Partelli, & Ramalho, 2018; Sui, Mao, Wang, Zhang, & Zhang, 2012; Wu, Chow, Liu, Shi, & Jiang, 2014). Our results demonstrate that the water irrigation volume applied to meet crop water needs (100% by SIC) favored black pepper growth.

At the end of the experiment, MSL reduced by 40% in plants under V1 when compared to the highest volume (Figure 4). The same behavior occurred for NL and LA, with reductions of 55 and 57%, respectively (Figures 5 and 6). However, SD was not significantly influenced by irrigation levels, but showed a growth trend, increasing by 12% between the lowest and highest volumes applied (Figure 3).

Our findings regarding the response patterns to water restriction of MSL values (Figure 4) were similar to those for bell pepper (Aragão et al., 2011) and habanero pepper (*Capsicum chinense Habanero*) (Pérez-Gutiérrez et al., 2017), both under water restriction.

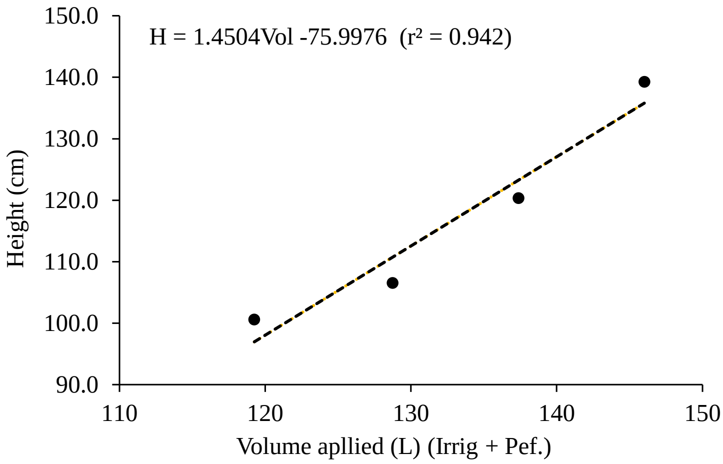

Figure 4. Growth in main stem length of black pepper plants (cv. Bragantina) as a function of the water volumes applied. *Significant at 5% probability level by F-test.

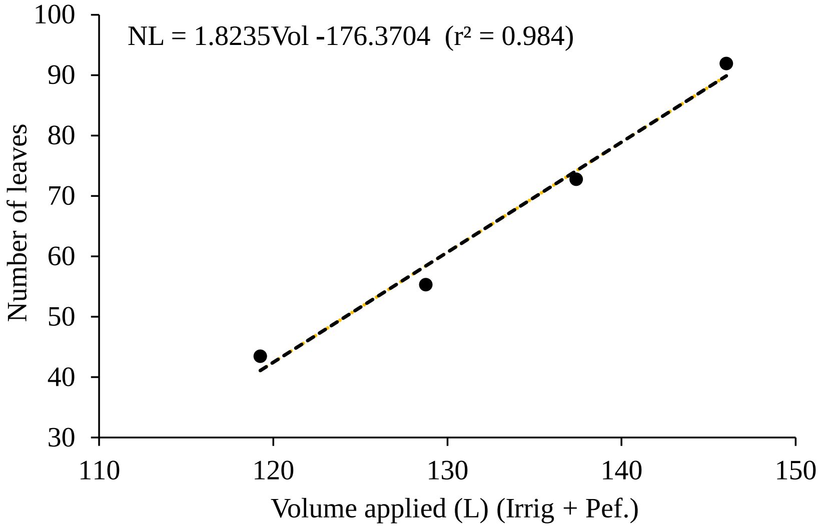

Figure 5. Increase in number of leaves of black peppers (cv. Bragantina) as a function of the total water volume received throughout the cultivation. *Significant at 5% probability level by F-test.

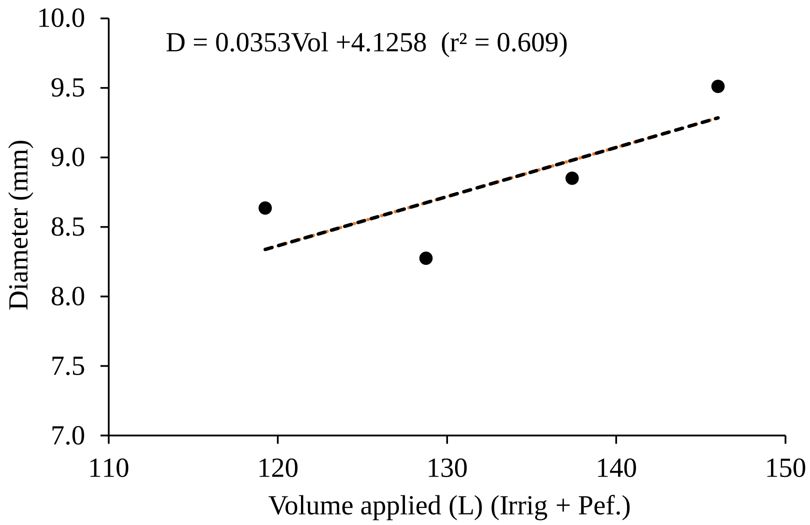

Figure 6. Leaf area increase in black pepper plants (cv. Bragantina) as a function of the total water volume received in the first year of cultivation. *Significant at 5% probability level by F-test.

Plants under V4 showed higher growth in MSL and consequently higher numbers of branches and leaves compared to the other treatments. On the other hand, plants under water deficit conditions (V1 and V2) showed leaf abscission (Figure 2), which may be related to plant mechanisms to avoid excessive water losses (Taiz, Zeiger, Møller, & Murphy, 2017; Oliveira et al., 2020; Valença et al., 2020).

Stomatal closure caused by water deficit and consequent reduction of carbon dioxide (CO_2) absorption can reduce photosynthetic activity and accumulation of photoassimilates (Taiz et al., 2017). Thus, this factor could be related to the marked reductions in MSL and NL observed here for the lowest irrigation volumes (Figures 4 and 5). Water stress conditions also reduced the leaf area (LA) of black peppers due to leaf abscission or leaf downsizing (Figure 6).

Rasanjali et al. (2019) also found that water stress reduces leaf size and number in black pepper plants. Similar results were observed for tomato and pepper crops, which showed LA reductions when under water deficit conditions (Koch et al., 2019; Cemek, Ünlükara, Kurunç, & Küçüktopcu, 2020).

Significant differences were observed ($p < 0.05$, F-test) only for CHL_b at 1623 ADD and for $CHL_{a/b}$ at 2415 ADD (Table 1), which corresponded to 120 and 180 days after transplanting (DAT), respectively.

When comparing the highest (V4) with the two lowest irrigation volumes (62 and 41% by SIC), reductions of 40 and 26% were observed, respectively. At 180 DAT, the $CHL_{a/b}$ ratio increased as irrigation volume decreased and was 22% higher at the lowest irrigation volume compared to the highest one. For the other days evaluated, chlorophyll indices showed no significant differences (Table 1).

Table 1. Falker chlorophyll index at 1623 and 2415 accumulated degree-days (ADD) of black pepper plants (cv. Bragantina) subjected to different irrigation volumes.

Treat.	1623 ADD				2415 ADD			
	CHL_a	CHL_b	CHL_{a+b}	$CHL_{a/b}$	CHL_a	CHL_b	CHL_{a+b}	$CHL_{a/b}$
V1	36. 9*a	12.9ab	49.9a	3.0a	26.7a	6.7a	32.3a	4.4a
V2	35.3a	11.5b	47.7a	3.0a	30.6a	8.5a	48.4a	3.8ab
V3	33.9a	13.1ab	46.5a	3.5a	29.9a	9.0a	38.9a	3.4b
V4	38.8a	16.2a	55.0a	2.7a	29.7a	9.0a	38.7a	3.4b
OM	36.2	13.4	49.8	3.1	29.2	8.3	39.6	3.8

Treat. – Treatments; OM - overall mean; *Means followed by the same letters in the column do not differ by the Tukey's test at 5% probability level; V1 - 2.2 L h^{-1}; V2 - 3.3 L h^{-1}; V3 - 4.3 L h^{-1}; V4 - 5.3 L h^{-1}; CHL_a - chlorophyll *a* content; CHL_b - chlorophyll *b* content; CHL_{a+b} - total chlorophyll content; and $CHL_{a/b}$ - ratio between CHL_a and CHL_b.

The greatest reduction in leaf CHL_b was observed in plants subjected to the highest water restriction, therefore under water stress (Long, Humphries, & Falkowski, 1994; Silva et al., 2014). This result corroborates the studies conducted by Massacci et al. (2008) and Ferrari, Paz, and Silva (2015), who reported reductions in chlorophyll concentrations and photosynthetic rates due to the lack of water in the vegetative stages of cotton (*Gossypium hirsutum*) and soybeans *(Glycine max* (L.) Merr.).

At 120 DAT, plants under V1 showed a slight increase in CHL_b content compared to plants under V2, and the same occurred for photosynthesis parameters (Figure 7a). This may be related to a cyclic effect of recovery in the treatment with the lowest irrigation volume (Valença et al., 2018).

As plants received a fraction of the irrigation from reference treatment (V4), those subjected to the other treatments grew relatively less and, consequently, required a lower water volume for maintenance of vital functions.

As plants receiving the largest water volume (without restriction) grow, they demand more water, thus the fraction of water received by other treatments has to increase as well. Since plants under V1 had practically no growth compared to the other treatments, they started to receive more water than needed and were no longer under stress for some time. After growth was resumed, plants had their water demands increased once more and may return to stress condition again. A similar cyclic stress pattern was observed for lettuce under an irrigation system similar to ours (Valença et al., 2018).

At 180 DAT, the $CHL_{a/b}$ ratio increased due to reductions in CHL_b in that period, especially in V1 treatment. Under drought conditions, CHL_b reduction tends to be greater than CHL_a reduction, increasing the $CHL_{a/b}$ ratio (Jaleel et al., 2009; Jain, Tiwary, and Gadre, 2010). This prevents damage to photosystem II (PSII) due to excess energy because CHL_b occurs mainly in this photosystem (Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009; Jaleel et al., 2009). For okra (*Abelmoschus esculentus* L. Moench) and tomato (*Solanum lycopersicum* cv. Optima), reductions in CHL_a, CHL_b and CHL_{a+b} contents under water restriction conditions were associated with fewer damages to PSII, as the amount of energy absorbed was limited (Farias et al., 2019; Rivero et al., 2014).

The functional (energy distribution) and structural parameters in the photosynthetic apparatus of black pepper plants subjected to different irrigation volumes were deduced by the JIP test at four collection times (Figure 7).

At 120 DAT, energy transfer, indicated by the reaction center (RC), showed increases by 10 to 30% in absorption energy flow (ABS/RC) for water restriction treatments compared to the control. This parameter indicates an apparent increase in antenna size. Similarly, the amount of energy dissipated in the form of heat (DI_0/RC) was 30 to 55% higher under the same situation. Both parameters showed no alteration at 238 DAT and slight increases (up to 20%) at 386 and 391 DAT.

The parameter that measures the flow of energy capture by RC, which can reduce quinone A (Q_A) [ET_0/RC], showed an increase at 238 DAT and a slight decrease in the following days, especially under the lowest water volume (41% by SIC). The same behavior, that is, increase at 238 DAT and decrease at 386 and 391 DAT, was observed for electron transport efficiency (ψEo), which was accompanied by the quantum yield for electron transport (φEo) (Figure 7).

In contrast, the efficiency with which an electron from the intersystem electron carriers moves to reduce end electron acceptors photosystem I (PSI) acceptor side [δRo] showed a slight decrease at 238 DAT and increases at 386 and 391 DAT. The (potential) performance index for energy conservation from exciton to the reduction of intersystem electron acceptors (PI_{abs}) and (potential) performance index for energy conservation from exciton to the reduction of end acceptors of PSI (PI_{total}) showed a decrease in all days evaluated, except at 238 DAT, which showed a 30% increase in PI_{abs} in treatments under water restriction. Water deficit caused a slight reduction in the maximum quantum yield of PSII (F_V/F_M) at 120 and 386 DAT.

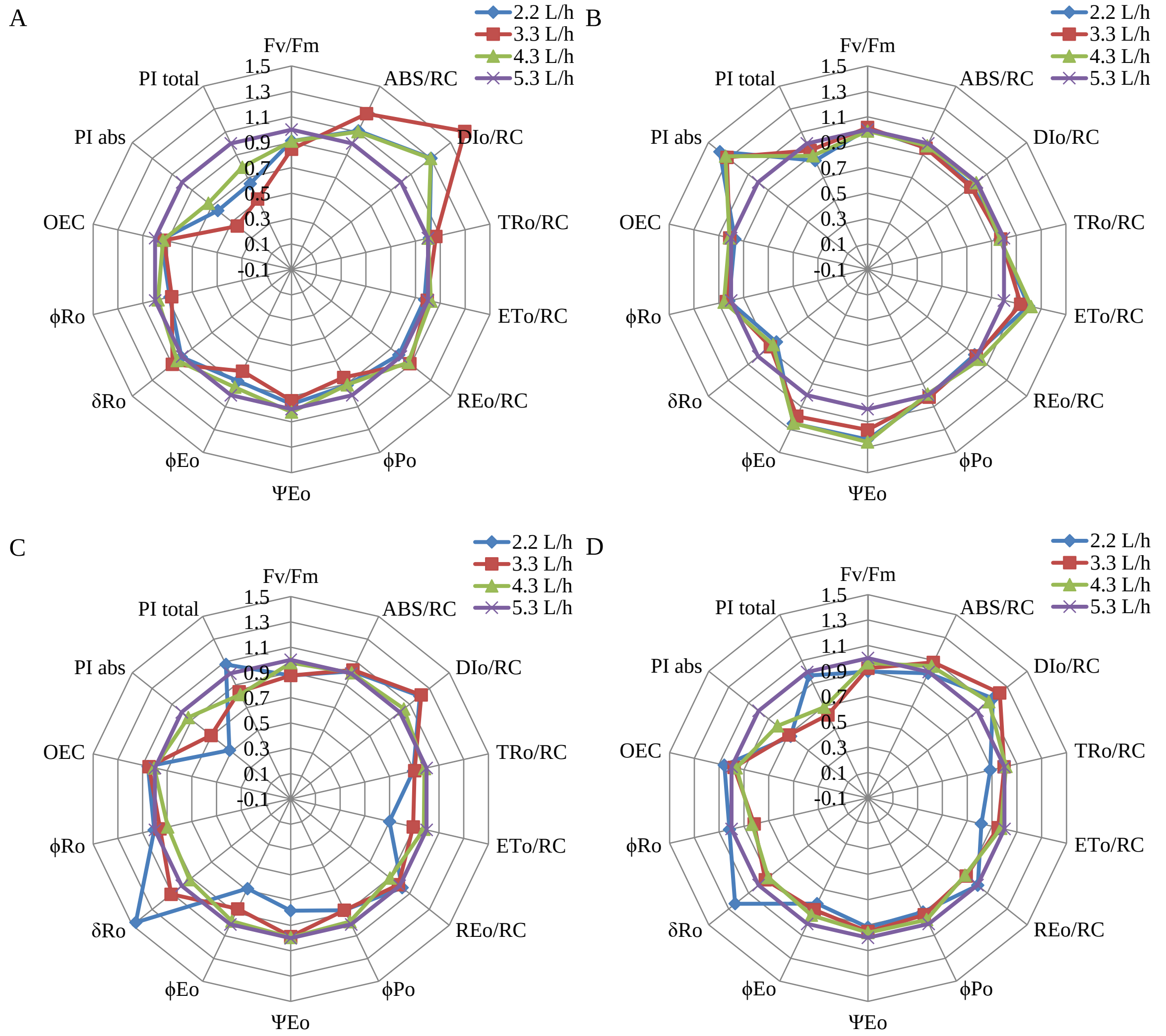

Figure 7. JIP-test-derived parameters of black pepper plants (cv. Bragantina) under different irrigation volumes at 120 (A), 238 (B), 386 (C), and 391 (D) days after transplanting (DAT. FV/FM: maximum photochemical efficiency; ABS/RC: energy fluxes for (light) absorption; DIo/RC: energy dissipation as heat per reaction center (RC); TRo/RC: trapping flux leading to quinone A (QA) reduction per RC; ETo/RC: electron trapping flux; RE0/RC: electron flux reducing end electron acceptors at the PSI acceptor side; ϕPo: maximum quantum yield for primary photochemistry; ψEo: efficiency/probability for electron transport (ET); ϕEo: quantum yield for ET; δRo: efficiency with which an electron of the intersystem electron carriers moves to reduce end electron acceptors at the photosystem I (PSI) acceptor side; ϕRo: quantum yield for reduction of end electron acceptors at the PSI acceptor side; OEC: oxygen-evolving complex; PIabs: partial performance index; and PI total: total performance index.

The reduction of F_V/F_M in plants subjected to the lowest irrigation volumes suggests partial photoinhibition, especially under V2 (Figure 7a). In this case, this photosynthetic efficiency reduction may be related to irrigation level reduction. Similarly, increases in ABS/RC and DI_0/RC reflect this process by increasing antenna size and energy loss as heat. The higher proportion between $DI_{0/RC}$ and ABS/RC increases suggests that part of the RCs may have been inactivated and modified into Q_A-non-reducing centers (Valença et al., 2020). PI_{abs} reductions with water restriction also reflect water deficit, with values well below those of the control plants. Such reduction may be indicative of impairment of primary photochemical reactions due to water scarcity (Borawska-Jarmulowicz, Mastalerczuk, Dąbrowski, Kalaji, & Wytrążek., 2020).

At 238 DAT, black pepper plants showed no alteration in virtually all photosynthesis parameters, except for PI_{abs}, which was 30% higher in plants under water restriction (Figure 7b). This finding indicates the recovery of plant photosynthetic parameters, which may be related to higher rainfall volumes during the period (Figure 1). After rehydration, plants previously subjected to drought conditions tend to show PI_{abs} increases if compared to plants that already had their water demands met (Borawska-Jarmulowicz et al., 2020). At 386 DAT, these plants showed stress effects again (Figure 7c) since the values of F_V/F_M decreased at the lowest irrigation volumes.

At 388 and 389 DAT, rainfall volumes of 8.8 and 8.0 mm were recorded, respectively, which may have met plant water needs. Thus, the photosynthesis parameters of treated plants were very close to those of the control (V4) on the last evaluation day (391 DAT), therefore, this volume was sufficient for their recovery (Figure 7d).

Conclusion

The results found in this study show that black pepper was very sensitive to water deficit because an irrigation volume reduction led to a proportional plant growth reduction. Water availability reduction also promoted changes in chlorophyll contents and energy use by the electron transport chain, characterizing plant stress. From 392 days onwards, our results contribute to understanding black pepper responses to water deficit, which can improve crop management conditions for this species.

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