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Morphological, physiological, and biochemical characteristics of Physalis peruviana L. plants under different water availabilities

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Abstract

Growing Physalis peruviana, which is known for its nutraceutical potential and pleasantly sweet-tasting fruits, can be a profitable economic activity for many small-scale farmers across different regions of Brazil. Therefore, studying its agronomic performance under adverse conditions is necessary, mainly concerning low water availability, which is common during dry periods in semiarid areas in the Northeast region of Brazil. Thus, the objective of this study was to assess the effects of different water availability conditions (20%, 40%, 60%, 80%, and 100% of field capacity - FC) on Physalis peruviana plants. Morphological and physiological characteristics were evaluated: plant height, stem diameter, primary root length, number of leaves per plant, leaf area, relative water content, leaf water potential, and total dry weight. Biochemical analyses were conducted to determine the contents of total soluble proteins, total sugars, reducing sugars, sucrose, and total chlorophyll. Plants subjected to 20% of FC exhibited reduced height, stem diameter, number of leaves, leaf area, relative water content, and leaf water potential due to low soil water availability. Water stress caused an increase in contents of chlorophylls, total soluble proteins, total sugars, reducing sugars, and sucrose.

Keywords: abiotic stress, cape gooseberry, field capacity, Solanaceae, water availability

Introduction

The genus Physalis (family Solanaceae) comprises approximately a hundred described species (Silva, 2014) distributed in tropical and temperate regions (Licodiedoff et al., 2013). The species Physalis peruviana L. is well-known for its pleasantly flavored fruits with a great nutritional and medicinal potential (Fisher & Miranda, 2012) and high commercial value, making it economically important and a profitable agricultural activity alternative for small-scale farmers. P. peruviana crops in Brazil is currently limited to the South and Southeast regions due to the varied climate conditions in the country and factors that can affect plant survival and maintenance (Lima 2009; Silva, et al., 2014).

Abiotic factors such as light, pH, and water availability are essential for plant survival; heir excess or scarcity cause plant stress to plants, affecting their growth and development. Considering commercially grown species, the challenge is even greater, as these factors can lead to reduced crop yields (Zanella, 2014).

Low water availability, also known as water deficit, is among the main factors affecting physiological and morphological responses in plants (Silva et al., 2009). Decreases in water potential caused by a low soil water content triggers several adaptive physiological responses, including the emergence of a reduced number of leaves and smaller leaf area (Ramos Júnior et al., 2013), as well as the accumulation of solutes, such as sugars, to promote osmotic regulation and maintain cell turgor (Lisar et al., 2012; Morando et al., 2014).

Few studies investigating the performance of Physalis species under water deficit are found. Reis Souza & Amorim (2009) and Leite et al. (2018b) assessed morphological and physiological responses of P. angulata plants grown under water deficit conditions in Feira de Santana, Bahia, Brazil, and found that the species exhibits

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significant survival strategies when grown under soil water deficit. Santos (2019) studied different soil water tensions for growing P. peruviana under field conditions in Diamantina, Minas Gerais, Brazil, and found that the most recommended irrigation management for growing this species in the studied soil should maintain soil moisture close to field capacity.

Considering the economic importance of this species, studies assessing its responses to different water availabilities can contribute to the development of techniques and management practices for growing this species in different regions of Brazil. Therefore, the objective of this study was to evaluate morphological, physiological, and biochemical characteristics of Physalis peruviana plants under different water availability conditions and determine the ideal field capacity for the growth of this species in pots.

Material and Methods

The experiment was conducted in a greenhouse at the Horto Florestal Experimental Unit at the State University of Feira de Santana (UEFS), Feira de Santana, Bahia, Brazil (12°14'S, 38°58'W, and 258 m of altitude), between February and June 2019.

Determination of irrigation water levels and evaluation of effects of water availability

The daily water consumption for each Physalis peruviana plant after 30 days of planting was determined to assess the effect of water availability. Initially, three pots were filled with 8 kg of air-dried soil, weighed, and irrigated with a known volume of water until saturation, sealed with a polyvinyl chloride (PVC) film, and suspended to drain excess water. These vessels were weighed again after 24, 48, and 72 hours; the weight difference was used to establish the field capacity (FC) of the soil and the water levels equivalent to 20%, 40%, 60%, 80%, and 100% of the retained water, following the methodology described by Bonfim-Silva et al. (2011).

Seedling production

The seedlings were produced using P. peruviana seeds from the seed bank of the Germination Laboratory (LAGER) of the UEFS. These seeds were placed in plastic tubes filled with commercial substrate, which were then subjected to automatic irrigation for 15 minutes twice a day. Seedlings measuring approximately 15 cm were transplanted 30 days after sowing into plastic pots (8-liter volume) filled with a sandy clay soil corrected to the ideal pH conditions.

The soil used was collected from the 0-20 cm layer, presenting the following physical and chemical characteristics before fertigation: pH = 5.9; sand, clay, and silt = 851, 90, and 59 g kg-1, respectively; Organic matter = 16 g dm-3; mmol dm-3 : Al3+ = 1, K = 1.8, Ca = 11, Mg = 5, and H+Al = 23 g dm-3; P = 16, S = 11, B = 0.46, Cu = 0.8, Fe = 83, Mn = 11, and Zn = 4.7 mg dm-3; base saturation = 65,8%. The soil pH was corrected by liming using dolomitic limestone.

Experiment conduction

Cultural practices

Fertigation was performed immediately after transplanting the seedlings, based on monitoring the electrical conductivity of the saturation extract (Oliveira et al., 2016), using a nutrient solution (pH 6.5) at 50% ionic strength, following the recommendations of Leite et al. (2017) for hydroponic growth of P. angulata. Vertical trellising of plants was conducted throughout the experimental period, using stakes and nylon strings as support. Temperature and relative humidity were measured daily using a digital thermos-hygrometer installed inside the greenhouse for characterizing the climatic conditions during the experimental period.

Application of treatments

The pots containing the transplanted plants were placed in a mesh greenhouse covered with plastic film, where they were kept until the end of the experiment, when the plants were subjected to morphological, physiological, and biochemical analyses. The plants were maintained under a water regime of 80% of FC during the first 25 days after transplanting (DAT); subsequently, the application of the different water availability treatments was started; all stablished water availability levels were reached at 30 DAT. The daily evapotranspiration of each pot was determined during the 35 days following the application of the treatments: three weighing replications per treatment were performed using an electronic balance (5 g); the weight difference was used as the basis for water replacement according to the established water availability for each treatment (Leite et al., 2018b).

The experiment was conducted in a completely randomized design, consisting of five treatments of water availability conditions (20%, 40%, 60%, 80%, and 100% of field capacity - FC) with twelve replications, totaling 60 experimental units (plants).

Assessments at the end of the crop cycle

Plants were collected at 65 DAT for determining morphological, physiological, and biochemical characteristics.

a) Morphological characteristics

Three experimental units from each treatment were used to determine the following morphological characteristics: plant height, stem diameter, number of leaves per plant, leaf area, primary root length.

Plant height (cm) was measured using a millimeter ruler from the ground to the plant apex. Stem diameter (mm) was measured from the main branch to the intersection with basal branches, using a digital caliper. Number of leaves per plant was determined by direct counting. Leaf area (cm²) was measured using a leaf area meter (LI-COR LI 3100). Primary root length (cm) was measured using a millimeter ruler after washing the roots in running water on a sieve.

b) Physiological characteristics

Three experimental units from each treatment were used for determining relative water content, leaf water potential, shoot dry weight, and total dry weight.

Relative water content (%) was determined in fully expanded leaves from the middle third of the plants. These leaves were collected at 8:00 a.m. Three (3) leaf discs were removed from them using a leaf disc punch, weighed on an analytical balance, and placed in test tubes containing distilled water. The discs were weighed after eight hours and then dried in an oven at 60 °C for 24 hours; subsequently they were weighed again. The data obtained for fresh weight (FW), turgid weight (TW), and dry weight (DW) (g) were used in the following equation to determine the relative water content (RWC), according to Weatherley (1950): $RWC = [(FW - DW)/(TW - DW)] \times 100$

Leaf water potential (MPa) was determined in the early morning period, in leaves collected from the middle third of the plants, using a Scholander chamber (PMS 1000, PMS Instrument, Corvallis, USA).

The determination of shoot dry weight (g) and total dry weight (g) involved separating the plants into shoot and root parts, drying the materials in an oven at 60 °C until constant weight, and weighing them on an analytical balance (0.001 g).

c) Biochemical characteristics

Fully expanded leaves were collected from the middle third of three plants from each treatment to determine the contents of the following biochemical characteristics: total chlorophyll, total soluble proteins, reducing sugars, total soluble sugars, and sucrose. The results of these parameters were expressed as milligrams per gram of fresh weight (mg g-1).

Total chlorophyll content (chlorophyll a + b) was determined using the methodology described by Tanan et al. (2017) for P. angulata plants. A leaf disc measuring 10 mm in diameter was removed from each leaf using a leaf disc punch. These discs were placed in test tubes containing 5 mL of ethanol reagent (95%), which were sealed with aluminum foil and kept at room temperature for 72 hours. Readings were then taken on a spectrophotometer (Femto 800XI, São Paulo, Brazil); wavelength and quantification determinations followed the equations proposed by Lichtenthaler (1987) for ethanol extracts.

Total soluble protein content was determined colorimetrically using by the Bradford method (Bradford, 1976), using bovine serum albumin (BSA) as the standard protein. Reducing sugars (RS) were quantified using the dinitrosalicylic acid (DNS) method, according to the methodology proposed by Miller (1959). Total soluble sugar content (TSSC) was quantified using the anthrone method (Yemm & Willis, 1954). Sucrose content was obtained according to the formula $S = TSSC - RS$.

Statistical analysis

The data obtained were subjected to analysis of variance, and the means of the water availability treatments were compared using the Tukey test at 5% probability, using the software SISVAR 5.6 (Ferreira, 2014).

Results anf Discussion

Morphological and physiological characteristics

Water deficit conditions directly affected leaf water potential, relative water content, growth, and dry weight accumulation in the evaluated Physalis peruviana plants (Figures 1, 2, 3, and 4). According to Taiz et al. (2017), water potential is a measure of the free energy of water within the plant, and the plant water status is a determining factor in processes such as cell growth, photosynthesis, and production in plants.

The water potential in plants corresponds to the amount of free water available for plant physiological activities; it decreases as the soil water availability is reduced (Marenco & Lopes, 2005). P. peruviana plants maintained under the most severe water deficit tested in the present study (corresponding to a 20% field capacity - FC) presented, on average, 70% lower water potential compared to well-hydrated plants, which had a higher amount of available free water.

Similar results have been reported in several studies evaluating the effects of water deficit on plant development. The plant water potentials found in these studies have shown a decreasing trend as water availability is reduced. Leite et al. (2018) evaluated P. angulata plants and found that those subjected to a water deficit of 20% of FC had lower water potential than those subjected to 40%, 60%, 80%, and 100% of FC, which did not differ significantly. Similarly, Vieira et al. (2014) reported that higher irrigation levels resulted in higher water potential for sugarcane plants, whereas low soil water availability resulted in lower water potentials.

Plants in the treatment with 20% of FC showed a mean leaf relative water content (RWC) of 61%, not differing significantly from that found in plants in the treatment with 40% of FC, but lower than those found for plants in the others treatments (**Figure 1**A). The lower water availability during the experimental period resulted in lower water potential and accumulation in leaf tissues of plants subjected to 20% and 40% of FC compared to those in treatments with 60%, 80%, and 100% of FC. Fioreze et al. (2011) subjected soybean genotypes to water deficit and found lower RWC due to low soil water availability compared to plants under abundant irrigation.

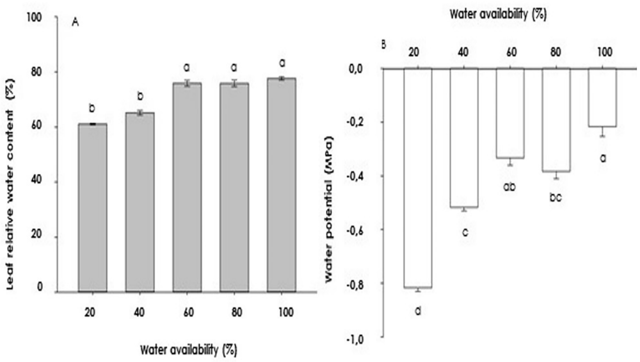

Figure 1. Leaf relative water content (RWC) (A) and water potential (B) of *Physalis peruviana* plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

The treatment with 20% of FC resulted in lower plant height (PH) and stem diameter (SD) compared to the other treatments (**Figure 2**A, B). However, the treatment providing the highest water availability (100% of FC) resulted in the highest mean PH and SD, differing significantly from the treatments with 40% and 20% of FC.

PH was significantly affected by the most severe water deficit, which resulted in a 35.5% lower PH compared to the treatment providing 100% of FC. The first physiological response of plants to water deficit is related to their growth. Low soil water availability decreases cell turgor, promoting reduced cell expansion and, consequently, plant growth (Ramazanzadeh & Asgharipour, 2011). Dos Reis Souza and Amorim (2009) and Leite (2019) found similar results when evaluating the effects of water deficit on the growth and development of P. angulata plants.

SD was also affected by low water availability.

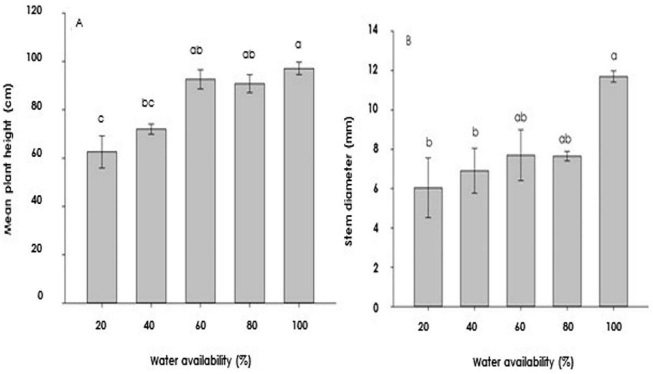

Figure 2. Mean plant height (cm) (A) and stem diameter (mm) (B) of *Physalis peruviana* plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

Plants subjected to treatments with 20% and 40% of FC had, on average, 45% smaller SD than those subjected to 100% of FC. However, plants under 100% of FC were more prone to lodging due to rotting of the stem base, which caused wilting and yellowing of the area, resulting in plant death due to excess water.

No significant difference was found for plant growth among the treatments with 60%, 80%, and 100% of FC. This denotes that maintaining these plants under 100% of FC is not necessary, as they respond positively in growth when subjected to water availability between 60% and 80% of FC.

The number of leaves per plant (NLP) is another parameter related to plant growth. Overall, NLP was proportional to the amount of water provided to the plants, showing a significant difference between the treatments with 20% and 100% of FC (**Figure 3**A). Morales et al. (2015) subjected two tomato lineages to water deficit conditions and found a trend of decrease in NLP as the water availability was reduced. The treatments with 60%, 80%, and 100% of FC presented no significant difference for leaf area (LA) but differed significantly from the treatment with 20% of FC, which resulted in plants with 64% smaller LA (Figure 3B).

Cell elongation is lower under low soil water availability conditions, affecting the growth of plant organs. A reduced LA due to soil water deficit is a plant mechanism for survival under water stress, as a smaller LA results in a smaller transpiration surface and, therefore, less water will be lost to the environment (Kerbauy, 2004).

The available water in the soil is absorbed by the roots and then participates in several processes in the plant, including growth, turgor, and cell division, promoting the development and growth of plant organs. Therefore, low soil water availability directly affects these processes, consequently decreasing dry biomass yield.

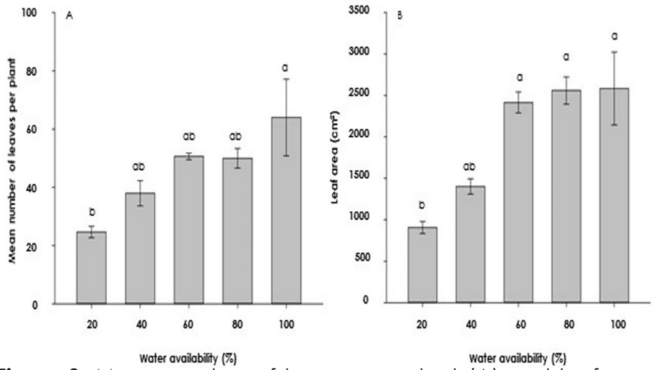

Figure 3. Mean number of leaves per plant (A) and leaf area (B) of *Physalis peruviana* plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

This was found for the evaluated P. peruviana plants, as those subjected to the highest water deficit presented, on average, 36% lower total and shoot dry weights than those in the treatment with 100% of FC (**Figure 4**). Similar results were found by Mauad et al. (2011) and Conceição Mar et al. (2014) for rice plants and açai trees subjected to water deficit, respectively.

Root dry weight (RDW) did not differ significantly among treatments (Figure 4C); however, primary root length (PRL) was affected by low water availability (Figure 4D). Plants under 20% of FC showed a 58% longer PRL than those under 60% and 100% of FC. A reduced soil water availability inhibits stem growth and leaf expansion. However, water deficit stimulates root elongation to reach water in deeper soil layers (Marostica, 2018), which may be a mechanism of P. peruviana plants to promote acclimation under stress conditions. Batista (2018) reported that sorghum (Sorghum bicolor L.) roots under water deficit conditions tend to grow vertically to reach water in deeper soil layers.

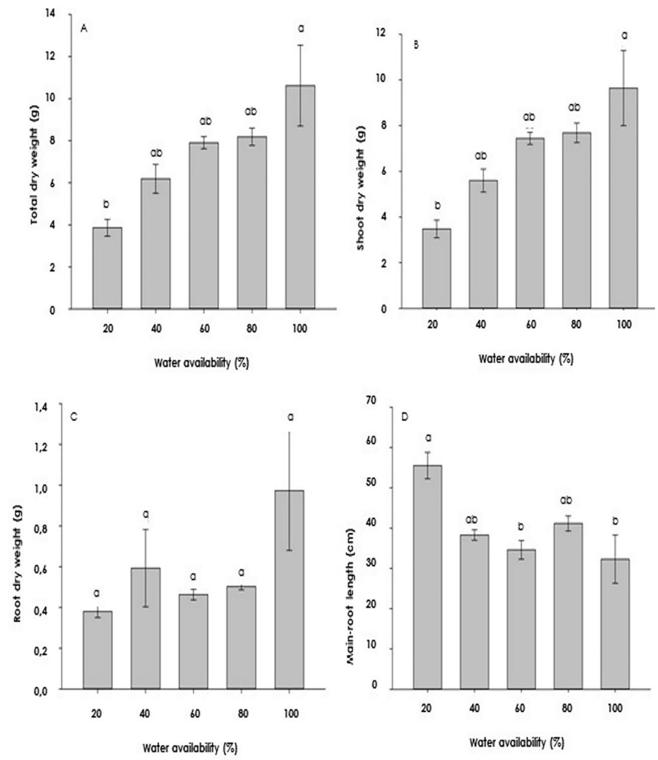

Figure 4. Total dry weight (A), shoot dry weight (B), root dry weight (C), and main-root length (D) of *Physalis peruviana* plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

Biochemical characteristics

Water stress caused the synthesis of photosynthetic pigments in the evaluated P. peruviana plants (**Figure 5**). The highest total chlorophyll content was found in plants under 20% of FC, differing significantly from the other treatments. Plants under 00% of FC had 30% lower total chlorophyll than those under water deficit, denoting that water restriction induces chlorophyll accumulation in P. peruviana leaves.

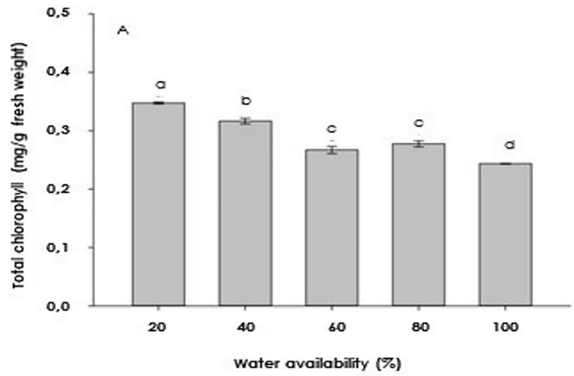

Figure 5. Total chlorophyll content in leaf discs of Physalis peruviana plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

Carvalho et al. (2003) highlighted that the increase in total chlorophyll in plants under water deficit may be indicative of stress. This difference can also be observed in leaf color. Plants subjected to irrigation at 20% of FC exhibited leaves with a darker green hue than those under the other water availability conditions, which can be attributed to the accumulation of this pigment in response to the imposed water deficit. Moura et al. (2016) studied Jatropha curcas L. plants under different irrigation levels and reported that those maintained under water deficit conditions showed had increased levels of photosynthetic pigments, which were higher than those found for the control plants (well-irrigated plants).

Other biochemical changes were found in the evaluated P. peruviana plants under different water availability conditions (**Figure 6**). The total soluble protein content (TSP) was affected as the water availability was reduced. Plants maintained under 80% and 100% of FC presented, on average, 33% lower TSP than those under 20% of FC, which presented the highest TSP, with no significant difference from the plants under 40% and 60% of FC.

The plants maintained under intense water deficit (20% of FC) also presented the highest total sugar contents, showing 47% higher means than those under irrigation at 60%, 80%, and 100% of FC. The treatments with 20% and 40% did not differ significantly from each other and presented the highest reducing sugar contents, but differed significantly from the other treatments (60%, 80%, and 100% of FC), which did not present significant differences. Similarly, sucrose contents in plants under irrigation at 20% of FC were, on average, 45% higher than those found for plants in the other treatments.

According to Muller (2012), plant tissue increases protein synthesis in response to changes in its cellular metabolism to ensure the maintenance and execution of its basic functions. The increase in reactive oxygen species

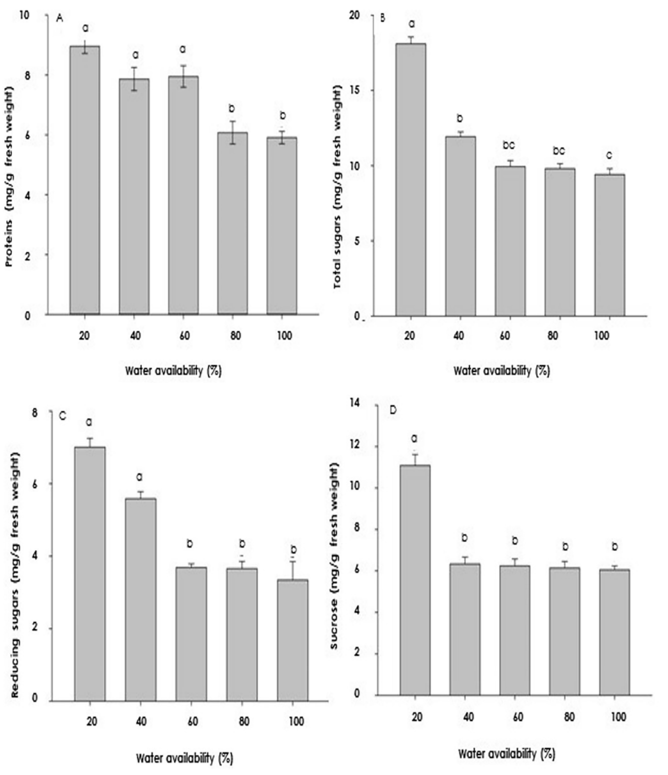

Figure 6. Contents of total soluble proteins (A), total sugars (B), reducing sugars (C), and sucrose (D) of *Physalis peruviana* plants subjected to different water availability conditions. Values are presented as mean ± standard error. Means followed by the same letter are not significantly different from each other at a 5% significance level.

in response to stress triggers the opening of calcium channels, increasing the concentration of this element and causing the activation of calcium-dependent proteins (Taiz et al., 2017) to ensure plant acclimation. Therefore, a reduced water potential under severe water stress induces an intense synthesis of total soluble proteins in P. peruviana leaves, possibly to ensure the stability of its metabolism under adverse environmental conditions.

Paixão et al. (2014) subjected sunflower plants to water stress and found a significant increase in total soluble protein contents as the plants' water potential decreased. Similarly, Mendes et al. (2011) found increases in protein contents as a strategy to promote the osmotic adjustment of the plant cells when evaluating the effects of salinity on ornamental pineapple plants.

Total soluble sugar, reducing sugar, and sucrose contents (Figure 6B, C, and D) were also directly affected by the treatments, increasing as the water availability was reduced. Plants intensify the production of solutes when under water stress conditions, storing them in the plant cells as a mechanism for osmotic adjustment. The increase in the quantity of solutes inside cells induces water to move from the less concentrated to the more concentrated medium, thus ensuring cell turgor pressure (Chaves, 1991; Premachandra, 1992; Marijaun & Bosh, 2013) to sustain plant growth.

This strategy ensures the maintenance of osmotic balance in plants with low water potential, thus avoiding dehydration and ensuring their survival under water stress. Leite (2019) subjected P. angulata plants to low soil water availability levels and found an increase in reducing sugar, total sugar, and sucrose contents compared to plants maintained under higher irrigation levels.

Conclusions

A severe water deficit reduces the leaf water potential and relative water content in Physalis peruviana plants, causing decreases in plant growth rate and biomass accumulation, as well as favoring the accumulation of total sugars, reducing sugars, sucrose, and total proteins within the cells. Additionally, the levels of photosynthetic pigments increase as the water availability is reduced. The analysis of the obtained data showed that a water availability of 60% of field capacity is ideal for growing this species under the tested experimental conditions.

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