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Original Article

Water deficit exposure: physiological and biochemical changes in *Physalis angulata* L. (Solanaceae)

Exposição ao déficit hídrico: mudanças fisiológicas e bioquímicas em *Physalis angulata* L. (Solanaceae)

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Abstract

The use of drought-tolerant species, such as *Physalis angulata* L., in regions subject to water scarcity is an important strategy for food security, although the duration of exposure to water deficit may affect plant performance. Therefore, the aim of this study was to evaluate the physiological and biochemical aspects of *Physalis angulata* under water deficit conditions. Plants were subjected to different levels of water availability (20, 40, 60, and 80%) and evaluated on days 1, 3, 5, 7, and 9, in a factorial design. Water status, gas exchange, and accumulation of organic solutes in the leaves were analyzed. There was interaction between the evaluated factors, with primary alterations in the plants' water status and gas exchange. Plants subjected to the most restrictive treatments showed reductions in relative water content, CO_2 assimilation, stomatal conductance, transpiration, and internal CO_2 concentration, but with increased water use efficiency in most of the evaluated periods. The accumulation of organic solutes, such as sugars and proline, increased under more severe water restrictions, with a peak on the fifth day of deficit, followed by a decline. Water deficit induced physiological and biochemical changes in *P. angulata*, with better responses observed in plants exposed to five days of water deficit.

Keywords: abiotic stress, gas exchange, organic solutes, semi-arid.

Resumo

A utilização de espécies tolerantes ao déficit hídrico, como *Physalis angulata* L., em regiões sujeitas à seca é uma estratégia importante para a segurança alimentar, embora a duração da exposição ao déficit possa afetar o desempenho das plantas. Portanto, o objetivo deste estudo foi avaliar os aspectos fisiológicos e bioquímicos de *Physalis angulata* em condições de déficit hídrico. As plantas foram expostas a diferentes níveis de disponibilidade hídrica (20, 40, 60 e 80%) e avaliadas nos dias 1, 3, 5, 7 e 9, em esquema fatorial. Foram analisados aspectos do status hídrico, trocas gasosas e acúmulo de solutos orgânicos nas folhas. Houve interação entre os fatores avaliados, com alterações primárias no status hídrico e nas trocas gasosas das plantas. As plantas submetidas aos tratamentos mais restritivos apresentaram redução no teor relativo de água, assimilação de CO_2, condutância estomática, transpiração e concentração interna de carbono, mas com aumento na eficiência do uso da água na maioria dos períodos avaliados. O acúmulo de solutos orgânicos, como açúcares e prolina, aumentou sob maiores restrições hídricas, com acúmulo máximo no quinto dia de déficit, seguido de declínio. O déficit hídrico promoveu mudanças fisiológicas e bioquímicas em plantas de *P. angulata*, com melhores respostas observadas em plantas submetidas a cinco dias de déficit hídrico.

Palavras-chave: estresse abiótico, trocas gasosas, solutos orgânicos, semiárido.

1. Introduction

Abiotic stresses, which have been intensified in recent years due to environmental changes, demand agronomic solutions to ensure food security (Sandalio, 2022). Drought is the main abiotic stress factor, and its effects depend on the duration of the water limitation period, as well as the intensity and frequency of exposure (González-Chavira et al., 2018), thereby limiting plant growth and development (Isiyel et al., 2025).

Understanding climatic variables is essential for the development of effective management strategies (Silva et al., 2023), as it requires anticipating actions to cope with climate-related challenges (Yomo et al., 2020). Addressing climatic constraints within the context of agro-food systems can enhance resilience in vulnerable regions, such as semi-arid environments (Dzvene et al., 2025).

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From this perspective, the use of regional plant resources is strategic (Leite et al., 2021; Silva et al., 2021; Lima et al., 2024; Santos et al., 2024), such as *Physalis angulata* L. (Solanaceae). *P. angulata* is considered an unconventional food plant in the region, still underutilized by the population but with potential for market integration. The important characteristics of the species, in addition to its food use (Kinupp and Lorenzi, 2014), include its agronomic aspects (Vargas-Ponce et al., 2016) and pharmacological applications (Rivera et al., 2018; Huang et al., 2020).

Studies carried out with *P. angulata* describe the species' responses to abiotic stress, such as water and salinity stress, which are limiting factors for plant growth and development, resulting in changes in gas exchange, osmotic adjustment and morphological traits (Leite et al., 2018; Silva et al., 2021) as well as the use of chemical priming as a plant sensitization strategy (Zhang et al., 2023), which also showed promising results (Leite et al., 2021).

However, there is no information regarding the influence of the duration of exposure to abiotic factors, such as water deficit, and how this factor may affect the responses of *P. angulata* to drought, which can serve as a basis for future work with the species under conditions of water deficit, in genetic improvement, including gene expression analysis, as well as providing guidance for farmers to use abiotic stress mitigators in the species at the appropriate time. In this context, we aimed to evaluate the physiological and biochemical aspects in *P. angulata* exposure to water deficit.

2. Material and Methods

2.1. Characterization of the study area and conduction of the experiment

The work was carried out at the "Horto Florestal", experimental unit of the State University of Feira de Santana (UEFS), 12º 16' 7.2" S and 38º 56' 21.6" W and 258 m above sea level. The experiment was carried out in a greenhouse with 50% shading. The microclimate conditions inside the greenhouse were obtained using a thermo-hygrometer (Figure 1), positioned at the height of the pots and adjusted to the height of the plant canopy during the course of the experiment.

A commercial substrate (Tropstrato®, Vida Verde, Brazil) was used in the experiment, composed of pine bark, peat and vermiculite, with a pH of 5.8 ± 0.3 and an electrical conductivity of 1.2 ± 0.3 mS/cm. The material was dried in the sun and then used to determine the maximum water availability of the potting mix (WA%). A total of 0.4 kg of dried substrate was used in 0.8 L pots. The pots were saturated by capillarity and sealed at the top with PVC film. After 24 hours, the pots were weighed again, and the maximum water availability was measured by mass difference.

Sowing was performed directly in the pots, with 3 seeds per pot, and thinning was carried out 5 days after seedling emergence. Irrigation took place twice a day, in the early morning and late afternoon, for 23 days. After this period, the plants were subjected to treatments with 20%, 40%, 60%, and 80% water availability (WA). The period of water deficit began when the plants in the most restrictive treatment reached the stipulated level of 20% WA. Consecutive days of water deficit were considered for the destructive sampling on days 1, 3, 5, 7, and 9.

A completely randomized design was used in a 4 x 5 factorial scheme, considering four water availabilities (20%, 40%, 60%, and 80%) and five days of exposure to water deficit (1, 3, 5, 7, and 9), with three replicates of each treatment, in which each replicate corresponded to one plant.

2.2. Relative water content

Evaluations and material collection began 28 days after sowing, when the first day of water deficit was recorded at 20% WA. The evaluation was conducted on fully expanded leaves from the middle third of the plants, ten 5-mm discs were collected to determine the fresh mass (FM, g), turgid mass (TM, g), and dry mass (DM, g) (Weatherley, 1950). The turgid mass was obtained by placing the discs in a Petri dish with distilled water for 5 hours. Dry mass

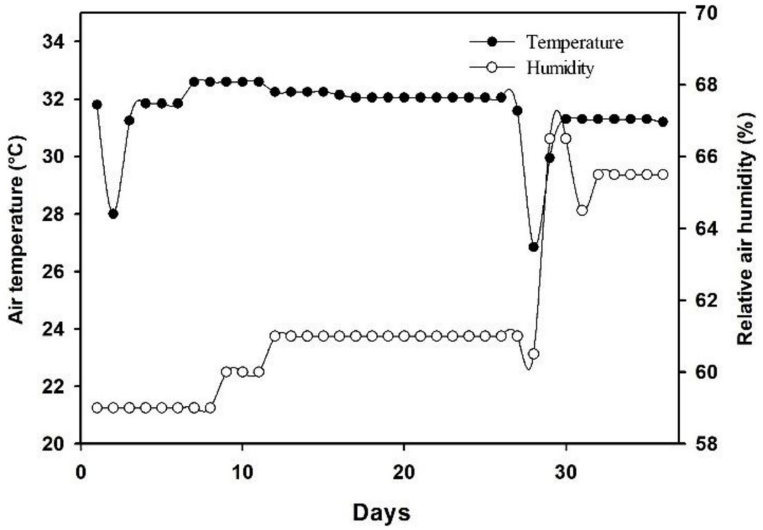

Figure 1. Microclimate inside the greenhouse showing the mean temperature and relative humidity.

was determined by drying the discs in a forced-air oven at 60°C until a constant mass was achieved.

2.3. Gas exchange

Photosynthesis was assessed using portable IRGA equipment (Portable Photosynthesis System LI-6400XT) between 9:00 and 11:00 a.m., under a photon flux density of 1200 µmol m^{-2} s^{-1}, and a chamber temperature of 25 °C, were taken 10 readings for each repetition at 10 s intervals. The following parameters were evaluated: CO_2 assimilation (A, µmol CO_2 m^{-2} s^{-1}), stomatal conductance (GS, mol H_2O cm^{-2} s^{-1}), internal carbon concentration (Ci, µmol CO_2 mol^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}) and leaf temperature (LT, ºC). Water use efficiency (WUE, mmol CO_2 $mmol^{-1}$ H_2O) was calculated from the CO_2 assimilation and transpiration data, considering the ratio A/E.

2.4. Biochemical determinations

The biomolecules were quantified in triplicates for each repetition, using extracts obtained by macerating 1 g of fresh leaf tissue in crucibles, adding 15 mL of 0.1 M potassium phosphate buffer (pH 7.0), and then centrifuging at 12,000 rpm for 15 minutes at 4°C. The supernatant was used for the evaluations.

Amino acid content (µg g^{-1} MF) was determined using the ninhydrin method (Yemm et al., 1955), total soluble sugars (µg g^{-1} MF) were determined using the anthrone method (Yemm and Willis, 1954), reducing sugars (µg g^{-1} MF) were determined using the dinitrosalicylic acid (DNS) method (Miller, 1959), and free proline levels (µg g^{-1} MF) were assessed according (Bates et al., 1973).

2.5. Statistical analysis

The obtained data were subjected to analysis of variance using the F-test. When a significant interaction between the factors was observed, a regression analysis was performed for water availability, and mean grouping was conducted using the Scott-Knott test at a 5% significance level for the factor day. Additionally, a multivariate principal component analysis (PCA) was conducted, focusing on the sampling day that exhibited the most pronounced responses to water restriction. The analysis also included chlorophyll Chl*a* and Chl*b* indices, measured using the portable ChlorofiLOG device. All analyses were performed in the R statistical software (R Core Team, 2021).

3. Results

Significant interactions were observed between water availability and days of exposure to water deficit for all the variables analyzed: relative water content, CO_2 assimilation, stomatal conductance, transpiration, internal CO_2 concentration, water use efficiency, leaf temperature, amino acids, free proline, total soluble sugars, and reducing sugars.

Thus, the interactions between the evaluated factors were analyzed by considering the relationship between water availability on each collection day and the effect of each day within the different levels of water availability.

3.1. Plant water status

There were significant changes in the water status of *P. angulata* plants subjected to water deficit (Figure 2 and Table 1). Thus, continued exposure to low water availability led to significant changes in the relative water content (RWC), with a positive linear adjustment for the third and ninth day of imposition of the deficit (Figure 2), corresponding to the lowest RWC values in the plants grown at 20% of the WA, 75.25% and 76.42%, respectively, and the highest at 80% of the WA, with respective increases in RWC of 15.14% and 16.31%. For days 5 and 7 of collection, there was a quadratic adjustment with higher RWC in the

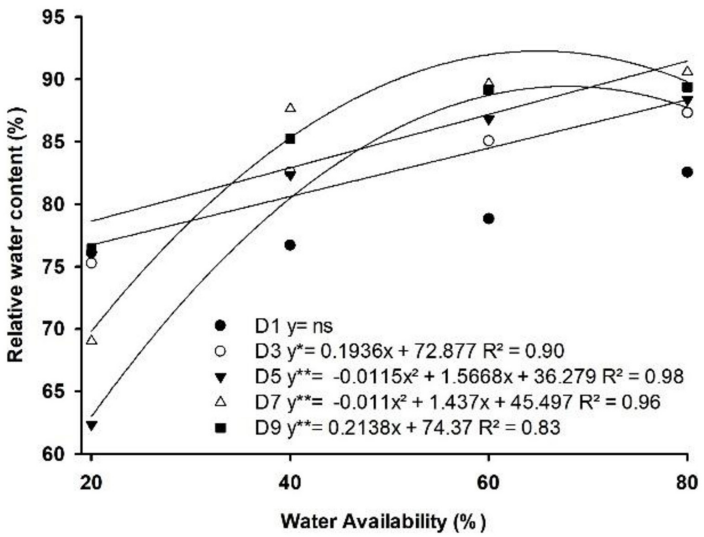

Figure 2. Relative water content of *Physalis angulata* subjected to different levels of water availability. Breakdown of the interaction between water availability and each evaluated day. D = day; ns = not significant; ** Significant at 1% probability by the *F test*; * Significant at 5% probability by the *F test*.

more hydrated treatments, the maximum points calculated corresponding to 68.12 and 65.31% of WA respectively.

The breakdown of the collection day interaction, considering each WA level (Table 1), showed that the higher water availability levels of 40%, 60% and 80% showed little variability. In contrast, the most restrictive treatment, 20% WA, showed significant variations over the days.

3.2. Gas exchange

There were significant variations in the gas exchange of *P. angulata* subjected to water deficit, considering the interaction between water availability and each collection day. For CO_2 assimilation on the first day of collection, there was a positive linear adjustment (Figure 3a) and a lower photosynthetic rate for plants grown at 20% WA, 2.23 µmol CO_2 m^{-2} s^{-1}, and higher rates in plants grown at 80% WA, corresponding to an increase of 448.65%. In addition, in the collections corresponding to days 3, 5, 7, and 9 (Figure 3a), quadratic adjustments were observed for CO_2 assimilation, with the lowest photosynthetic rates observed in the 20% WA treatment, and the highest values for 80% WA. In plants cultivated under 20% of WA, the following photosynthetic rates were measured over the evaluation days D3 - 3.85, D5 - 6.68, D7 - 5.63, and D9 - 4.09 µmol CO_2 m^{-2} s^{-1}. The following rates were determined for plants growing under conditions of good hydration 80% of WA: D3 - 14.39, D5 - 13.16, D7 - 12.40, and D9 -13.75 µmol CO_2 m^{-2} s^{-1}. The points of maximum CO_2 assimilation calculated for days 3, 5, 7, and 9 correspond to 73.54, 99.00, 71.70 and 100% of WA, respectively.

Analyzing stomatal conductance (Figure 3b), there was a positive linear adjustment for days 1, 5 and 9, in which plants grown at 20% WA showed the following conductance values: D1 - 0.084, D5 - 0.161 and D9 - 0.051 mol H_2O cm^{-2} s^{-1}. In relation to these evaluation days, plants grown at 80% WA showed increases in stomatal conductance of 740.74%, 564.71% and 1,200%, respectively. On collection days 3 and 7, the best significant fit was quadratic, with the highest values observed in plants grown at 80% RH, corresponding to D3 - 0.669, D7 - 0.657 mol H_2O cm^{-2} s^{-1}. The maximum points calculated for the respective collection days were 66.00% and 68.00% of the WA.

For leaf transpiration (Figure 3c), there was a quadratic adjustment on collection days 1, 3, and 7, with the highest transpiration values observed in the treatment with the highest WA, corresponding to D1 - 9.047, D3 - 11.336 and D7 - 9.819 mmol H_2O m^{-2} s^{-1}. The maximum points calculated for the respective collection days were 100%, 71.61%, and 73.10% of the WA. Evaluating days 5 and 9, the fit was positive linear, with the highest transpiration averages at 80% of WA, increases of 133.27% and 388.84% in relation to the lowest WA.

The internal carbon concentration (Figure 3d) showed significant changes from the third day of evaluation. There were significant quadratic adjustments for days 3, 7 and 9 with the highest internal carbon concentration at 60% WA, with 191.72 µmol CO_2 mol^{-1}, for the third day, while at 80% WA, for days 7 and 9, corresponding to internal carbon concentration of 266.07 and 277.63 µmol CO_2 mol^{-1}, respectively, the maximum points calculated for the third, seventh and ninth day were 64.72%, 66.79%, and 73.01% of WA respectively. On the fifth day there was a positive linear adjustment with the highest average at 80% of WA, 215.81 µmol CO_2 mol^{-1}, an increase of 21.15% compared to the lowest water availability.

Significant changes in water use efficiency were also observed, with a positive linear adjustment for the first day of collection (Figure 3e), in which the treatment with the highest water availability showed a measured value of 1.19 mmol CO_2 $mmol^{-1}$ H_2O, an increase of 43.80% compared to the 20% WA treatment. On the other hand, the efficiency of water resource utilization for days 3, 7, and 9 of evaluation (Figure 3e) showed a decreasing linear adjustment with greater efficiency in water utilization in the more restrictive 20% WA treatment, corresponding to D3 - 1.79, D7 - 1.77 and D9 - 2.90 mmol CO_2 $mmol^{-1}$ H_2O, with a decrease of 30.30%; 28.42% and 33.61% for the treatment with greater water availability. On the fifth day of evaluation (Figure 3e), there were no significant changes in water use efficiency.

Analyzing leaf temperature, there was a significant effect, with a negative linear adjustment for all the days evaluated (Figure 3f). Leaf temperature was higher in the treatment with plants grown at 20% water availability, D1 - 32.97, D3 - 32.04, D5 - 34.49, D7 - 30.44 and D9 - 30.91 ºC, which represented a decrease of 7.76%, 6.14%, 9.59%, 3.02% and 3.54% compared to plants grown at 80% WA.

When analyzing the interaction between collection days and water availability levels, significant contrasts

Table 1. Relative water content of *Physalis angulata* subjected to different water availability levels. Breakdown of the interaction by day (DIA) within each water availability level (WA).

Relative water content (%)				
	Water availability (%)			
Day	20	40	60	80
1	76.102 a	76.737 a	79.660 a	82.571 a
3	75.252 a	82.578 a	85.077 a	87.329 a
5	62.364 b	82.382 a	86.832 a	88.380 a
7	69.048 b	87.641 a	89.662 a	90.595 a
9	76.429 a	85.267 a	89.153 a	89.386 a

Means followed by the same lowercase letter in the column do not differ significantly according to the Scott-Knott test ($p < 0.05$).

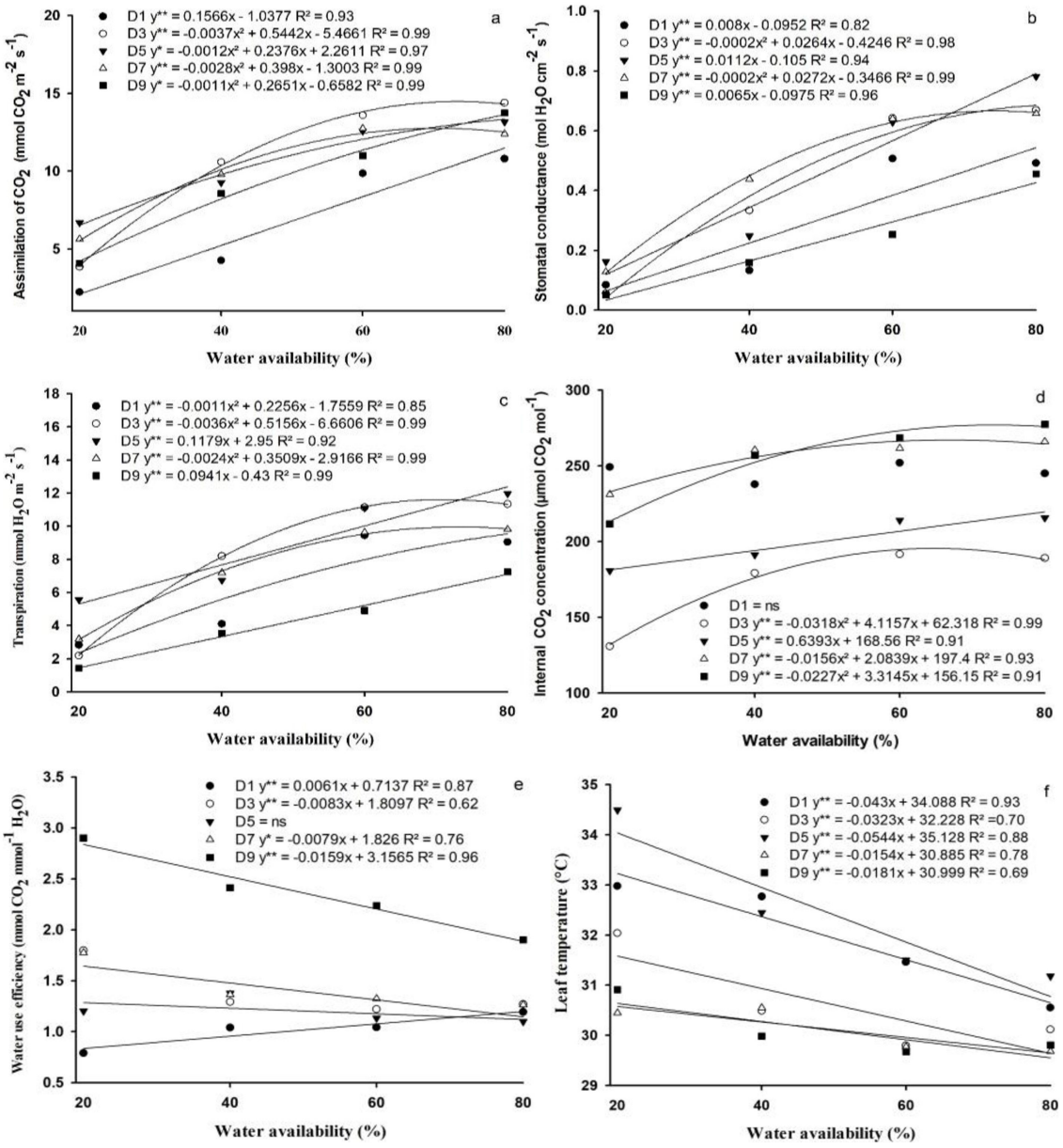

Figure 3. Gas exchange in *Physalis angulata* leaves under water deficit: CO_2 assimilation (a), stomatal conductance (b), transpiration (c), internal CO_2 concentration (d), water use efficiency (e) and leaf temperature (f). Breakdown of the interaction between water availability and each day evaluated. D = day; ns = not significant; **Significant at 1% probability by the F test; *Significant at 5% probability by the F test.

were observed in CO_2 assimilation (Table 2). At a WA of 20%, days 5 and 7 differed from the others, at a WA of 40%, days 3 and 7 showed significant differences, at a WA of 60%, days 3, 5, and 7 exhibited the highest values; and at a WA of 80%, days 3, 5, and 9 were grouped with the highest significant means compared to the other periods analyzed.

Stomatal conductance was significantly influenced by the day of evaluation and the level of water availability. At the lowest WA level (20%), days 5 and 7 (Table 2), exhibited significantly higher conductance compared to the other days, based on mean groupings. As water availability increased to 40%, greater conductance was observed on the seventh day, differing from the others. At 60% WA, days 3, 5, and 7 (Table 2) showed the highest significant averages. At the highest WA level (80%), day 5 (Table 2) showed the highest average.

Considering the leaf transpiration of plants grown at 20% WA (Table 2), the highest significant mean was observed on the fifth day of deficit. At 40% WA, the highest significant mean occurred on the third day, while at 60% WA, it was observed on the third and fifth days. In the treatment with the highest water availability 80% WA, the fifth day showed the highest significant contrast.

For the analysis of internal carbon concentration, significant changes were observed at 20% WA, with the highest mean recorded on day 1 (Table 2). At 40% WA, the highest grouped means were observed on days 7 and 9 (Table 2), which was the same pattern observed at 60% WA. In the treatment with the highest water availability 80%, the highest value was recorded on day 9 (Table 2).

Table 2. Gas exchange in *Physalis angulata* leaves under different water availability levels: CO_2 assimilation, stomatal conductance, transpiration, internal CO_2 concentration, water use efficiency, and leaf temperature. Breakdown of the interaction between days within each water availability level.

CO_2 assimilation (μmol CO_2 m^{-2} s^{-1})				
Water availability (%)				
Day	**20**	**40**	**60**	**80**
1	2.231 c	4.266 c	9.867 c	10.804 c
3	3.855 b	10.596 a	13.592 a	14.396 a
5	6.689 a	9.265 b	12.574 a	13.169 a
7	5.638 a	9.796 a	12.756 a	12.408 b
9	4.093 b	8.570 b	11.003 b	13.752 a
Stomatal conductance (mol H_2O cm^{-2} s^{-1})				
1	0.084 b	0.133 d	0.507 b	0.492 c
3	0.056 b	0.333 b	0.642 a	0.669 b
5	0.161 a	0.248 c	0.629 a	0.781 a
7	0.128 a	0.438 a	0.639 a	0.657 b
9	0.051 b	0.159 d	0.252 c	0.456 c
Transpiration (mmol H_2O m^{-2} s^{-1})				
1	2.827 c	4.099 d	9.463 b	9.047 d
3	2.181 d	8.191 a	11.141a	11.336 b
5	5.570 a	6.728 c	11.104 a	11.968 a
7	3.180 b	7.190 b	9.635 b	9.819 c
9	1.417 e	3.540 e	4.908 c	7.236 e
Internal CO_2 concentration (μmol CO_2 mol^{-1})				
1	249.321 a	237.999 b	252.114 b	245.055 c
3	130.877 e	179.224 c	191.728 d	189.229 e
5	180.804 d	191.325 b	214.165 c	215.813 d
7	231.290 b	260.553 a	261.751 a	266.076 b
9	211.785 c	257.154 a	268.580 a	277.636 a
Water use efficiency (mmol CO_2 $mmol^{-1}$ H_2O)				
1	0.789 d	1.041 c	1.042 b	1.192 b
3	1.797 b	1.293 b	1.219 b	1.269 b
5	1.201 c	1.378 b	1.132 b	1.099 b
7	1.776 b	1.364 b	1.323 b	1.264 b
9	2.900 a	2.413 a	2.238 a	1.902 a
Leaf temperature (ºC)				
1	32.977 b	32.770 a	31.462 a	30.549 b
3	32.041 c	30.490 c	29.797 b	30.117 c
5	34.494 a	32.446 b	31.504 a	31.180 a
7	30.366 e	30.552 c	29.773 b	29.678 d
9	30.910 d	29.984 d	29.675 b	29.808 d

Means followed by the same lowercase letter in the column do not differ significantly according to the Scott-Knott test ($p < 0.05$).

Water use efficiency was highest on the last day of analysis (Table 2) across all levels of water availability. Leaf temperature (Table 2) varied significantly within each treatment level, with the highest temperature recorded on day 5 at 20% WA, on day 1 at 40% WA, on days 1 and 5 at 60% WA, and on day 5 in plants grown at 80% WA.

3.3. Biochemical aspects

Significant changes were observed in the accumulation of organic solutes in *P. angulata* leaves. Considering the interaction of water availability across the collection days for amino acid content (Figure 4a), significant differences were observed. On the first day of collection, a positive linear trend was observed, with an increase in amino acids as water availability levels increased. Plants irrigated at 80% WA showed 47.61 μg.g^{-1}, a 26.07% increase compared to plants grown under the lowest water availability. On day 3, no significant changes were observed, while significant changes with a negative linear trend were noted for days 5, 7, and 9 of collection. On these days, plants grown at 20% WA exhibited higher amino acid content D5 - 60.75, D7 - 48.73, D9 - 37.86 μg·g^{-1}, with decreases of 41.39%, 64.61%, and 60.04%, respectively, compared to plants grown under the highest water availability.

Proline content was significantly affected by water availability only on collection days 3, 5, 7, and 9 (Figure 4b), where a negative linear trend was observed. The proline content was 110.45 μg·g^{-1} on day 3, 369.11 μg·g^{-1} on day 5, 228.59 μg·g^{-1} on day 7, and 154.16 μg·g^{-1} on day 9, with decreases of 96.92%, 109.67%, 119.96%, and 120.70%, respectively, compared to the proline content on the same days in plants grown at the highest WA.

A significant linear trend was observed for collection days 1, 3, 5, 7, and 9 in terms of total soluble sugars (Figure 4c), with a negative linear trend and greater accumulation in the treatment with the lowest WA of 20%. The total soluble sugar content was 55.50 μg·g^{-1}, on day 1, 72.83 μg·g^{-1} on day 3, 123.51 μg·g^{-1} on day 5, 85.75 μg·g^{-1} on day 7, and

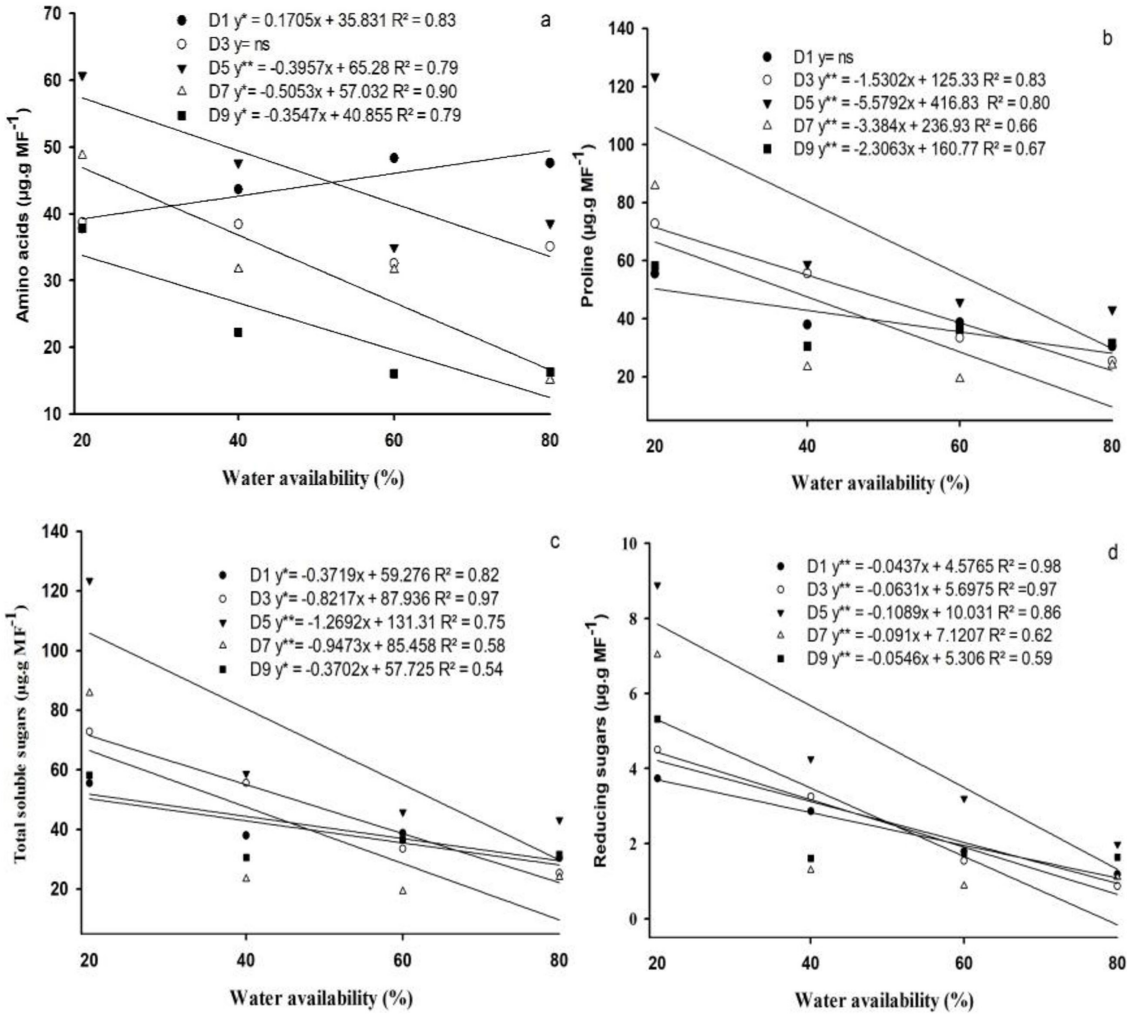

Figure 4. Accumulation of organic solutes in *Physalis angulata* subjected to different water availability amino acids (a), Proline (b), total soluble sugars (c) and reducing sugars (d). D = day; ns = not significant; ** Significant at 1% probability by the *F test*; * Significant at 5% probability by the *F test*.

58.22 μg·g^{-1} on day 9, with respective decreases of 44.00%, 68,95%, 71.89%, 85.46%, and 44.13% for the treatment with 80% WA. Reducing sugars (Figure 4d) exhibited a similar pattern to soluble sugars, with significant changes and a negative linear trend on all collection days. The reducing sugar content was 3.73 μg·g^{-1} on day 1, 4.50 μg·g^{-1} on day 3, 8.89 μg·g^{-1} on day 5, 7.02 μg·g^{-1} on day 7, and 5.32 μg·g^{-1} on day 9 in the most restrictive treatment, with decreases of 70.82%, 85.36%, 83.20%, 103.01%, and 77.74%, respectively, for the treatment with the highest WA.

Considering the interaction of evaluation days within each WA level (Table 3), significant changes were observed in amino acid content. The highest content was recorded on the fifth day at 20% WA, while at 40% WA, the highest significant contents were observed on days 1, 3, and 5. For water availability levels of 60% and 80%, the highest significant contents were observed on the first day of collection. The content of free proline was significantly affected only at 20% and 40% WA, with the highest contents observed on day 5 for 20% WA and on days 1 and 5 for 40% WA.

When analyzing total soluble sugars (Table 3), there were significant changes at the 20 and 40% water availability levels, the former with the highest average at 5 days, and the latter at 3, and 5 days. Reducing sugars (Table 3) showed greater significant contrasts at 20% WA at 5 days, at 1, 3, and 5 days for 40% WA, and 5 days for 60% WA.

3.4. Principal component analysis

From this perspective, the performance of *P. angulata* grown under different water availability levels and evaluated over nine days is complex, with the most pronounced responses observed on the fifth day of evaluation (Figure 5).

The principal component analysis (1 and 2) corroborates 98.33% of the results from the collection on the fifth day of evaluation, revealing that the accumulation of organic solutes and the chlorophyll *a* and *b* indexes are directly related to the severe soil water deficit of 20% WA. Meanwhile, the moderate deficit favored greater water use

Table 3. Accumulation of organic solutes in *Physalis angulata* subjected to different water availability amino acids, free proline, total soluble sugars and reducing sugars. Breakdown of the interaction between day and each level of water availability.

Amino acids μg g^{-1} FM				
	Water availability (%)			
Day	**20**	**40**	**60**	**80**
1	37.800 c	43.672 a	48.335 a	47.611 a
3	38.744 c	38.464 a	32.562 b	35.115 b
5	60.758 a	47.641 a	34.982 b	38.597 b
7	48.733 b	31.677 b	31.589 b	15.079 c
9	37.867 c	22.264 b	16.052 c	16.288 c
Proline μg g^{-1} FM				
1	77.614 c	72.876 a	62.255 a	59.150 a
3	110.457 c	47.712 b	19.117 a	17.973 a
5	369.117 a	123.856 a	30.065 a	28.431 a
7	228.594 b	22.222 c	14.542 a	5.555 a
9	154.166 c	16.667 c	7.516 a	3.464 a
Total soluble sugars μg g^{-1} FM				
1	55.505 c	23.397 b	38.740 a	30.465 a
3	72.830 b	30.594 a	33.525 a	25.423 a
5	123.513 a	38.007 a	45.851 a	43.222 a
7	85.759 b	55.634 b	19.217 a	24.001 a
9	58.220 c	58.823 b	36.456 a	31.586 a
Reducing sugars μg g^{-1} FM				
1	3.735 c	2.866 a	1.785 b	1.183 a
3	4.505 c	3.251 a	1.542 b	0.866 a
5	8.895 a	4.256 a	3.207 a	1.984 a
7	7.026 b	1.288 b	0.866 b	1.099 a

Means followed by the same lowercase letter in the column do not differ significantly according to the Scott-Knott test ($p < 0.05$). FM = fresh mass.

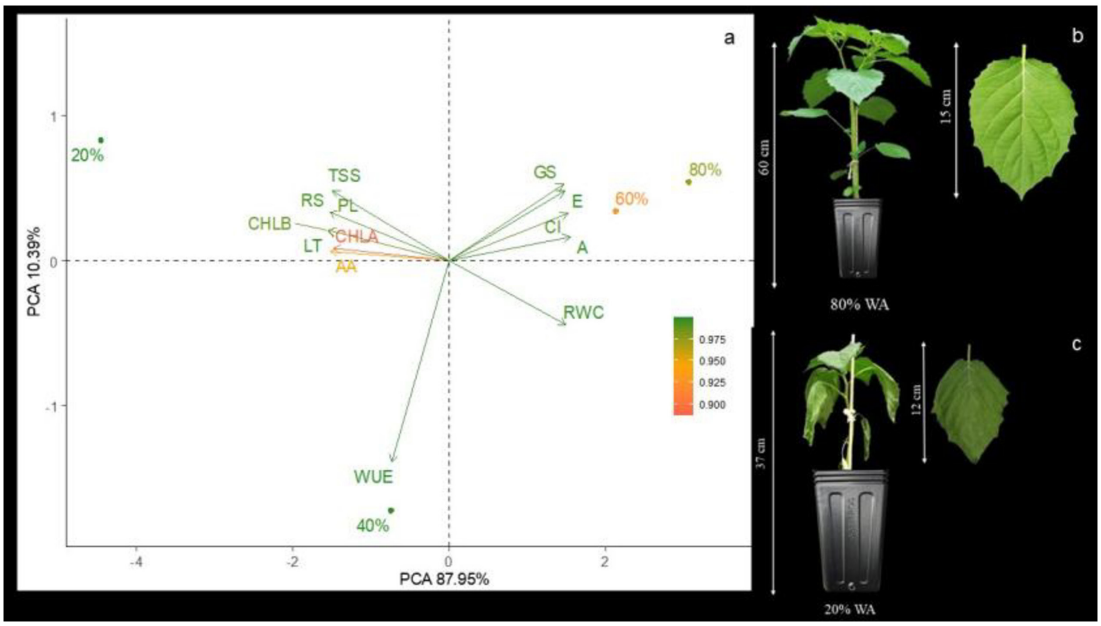

Figure 5. Principal components analysis for the fifth day of water deficit exposure in *Physalis angulata* (a), well-watered plant (b), and water deficit plant (c). TSS= Total soluble sugars; RS= Reducing sugars; PL= Proline; Chl*a*= *Chlorophyll index Chla;* Chl*b*= *Chlorophyll index Chlb*; LT= Leaf temperature; AA= Amino acids; WUE= Water use efficiency; RWC= Relative water content; A= CO_2 assimilation; CI= Internal CO_2 concentration; E= Transpiration; GS= Stomatal conductance.

efficiency. Aspects related to gas exchange and relative water content were more directly related to the higher hydration levels of 60% and 80%.

4. Discussion

Our work demonstrates that the performance of *P. angulata* grown under water deficit conditions shows temporal changes in biochemical and physiological aspects, mainly resulting in a reduction of evaluation time after the imposition of water restriction. This is an important factor for reducing costs in future experimental studies, as well as ensuring that future work avoids both underestimated and overestimated results.

4.1. Plant water status

Considering the interactions between water availability and each collection day (Figure 2), it is evident that changes in plant water status depend on the duration of exposure to water deficit. The initial exposure period to low water availability (first day of deficit) did not lead to significant water loss in plants in relation to their maximum water storage capacity in leaf tissues. Additionally, the interaction between collection days and each water availability level (Table 1) indicates greater stability in maintaining RWC under higher water availability levels, however plants grown at 20% soil moisture content exhibited greater variation.

Changes in the RWC of plants subjected to water deficit are the result of alterations in plant metabolism (Martins et al., 2024). According to Suriya-Arunroj et al. (2004), relative water content is related to osmotic adjustment to maintain cellular hydration. This is an important strategy during water deficit events, the response to which is species-dependent. Plants of *Lotus corniculatus* L. showed little influence of water availability on RWC (González-Espíndola et al., 2024), while *T. fruticosum* was highly influenced by water availability (Santos et al., 2024).

In *Physalis angulata*, the maintenance of high RWC in response to water deficit was associated with the species' ability to keep tissues hydrated and the plants' ability to rehydrate in deficit during the night (Leite et al., 2018), which was also observed in this work. Changes in the plant water status were also observed in *Physalis peruviana* under reduced water availability, which resulted in a significant reduction in RWC (Lima et al., 2024), and in grafted tomato plants subjected to different water regimes (Alves et al., 2021).

4.2. Gas exchanges

The gas exchange in *Physalis angulata* plants (Figure 3), considering the effects of water availability on each collection day, highlights an increase in CO_2 assimilation (Figure 3a), stomatal conductance (Figure 3b) and transpiration (Figure 3c), with an increase in water availability, which favors carbon gain. However, there was also an increase in internal carbon concentration (Figure 3d).

The data from the interaction between the days of collection and each level of water availability (Table 2) shows that the plants grown at 20% WA show changes in CO_2 assimilation as a function of the days of exposure. Plants grown under the greatest water restriction exhibited

higher photosynthetic rates on the fifth day of evaluation, with an increase up to day 5, followed by a subsequent decrease on days 7 and 9. However, plants grown under better water availability conditions (60 and 80% WA) also showed an increase in CO_2 assimilation compared to the first day of analysis, which may be related to the influence of environmental factors such as light during the evaluation period.

Stomatal conductance and transpiration were higher at the 20% WA level on days 5 and 7 for conductance and day 5 for transpiration, at the other WA levels, the changes seen in both aspects may be associated with climatological factors.

The impact of drought on photosynthesis occurs in the light-dependent reactions needed to generate ATP and NADPH and the independent ones, which correspond to carbon fixation and sugar synthesis from ATP and NADPH (Qiao et al., 2024), interfering with the enzymatic activity of RuBisCO (Batista et al., 2023). It is accepted that increased water restriction promotes stomatal closure and consequently a reduction in net photosynthetic rate (Medrano et al., 2002; Munjonji and Ayisi, 2021), in addition, stomata control water loss in plants by influencing transpiration and CO_2 assimilation (Yan et al., 2016). Consequently, reduced CO_2 assimilation affects 13 C discrimination (Munjonji and Ayisi, 2021).

Significant decreases in gas exchange, CO_2 assimilation, stomatal conductance, transpiration, and internal carbon concentration were observed in *Physalis angulata* subjected to water deficit (Leite et al., 2018, 2019, 2021), and salinity (Silva et al., 2021). However, this study points out that the changes triggered in photosynthesis, especially in the treatment with the greatest restriction of 20% WA, and depend on the duration of exposure to water deficit at a level sufficient to affect carbon gain (Figure 3 and Table 2).

Water use efficiency (Figure 3e) highlights the complexity and importance of evaluating both factors. Therefore, studies related to water restriction should consider exposure to water deficit as an important factor in choosing the evaluation period so as not to underestimate the analyses. Our work shows that on the first day of exposure to water deficit (Figure 3e), there were no physiological changes towards greater efficiency in the use of the water resource in the treatments with the greatest restriction of 20 and 40%, although there was a decrease in CO_2 assimilation and transpiration (Figures 3a and 3c). On subsequent days 3, 7 and 9 (Figure 3e), there was greater efficiency in water use in the lower WA treatment. However, on the fifth day of deficit, the water use efficiency (WUE) was not significant between the treatments.

In a strategic way, plants tend to increase their water use efficiency in conditions of low water availability in order to maintain RWC, even in deficit conditions (Qiao et al., 2024). This result is observed in other studies in water deficit conditions (Santos et al., 2024; Navegantes et al., 2024) including *P. angulata* (Leite et al., 2018). Under combined salinity and water deficit stress, a higher efficiency in water use was also observed in the treatments subjected to greater restriction (Ribeiro et al., 2024).

Leaf temperature was influenced by water availability treatments and days of exposure to water deficit, with higher temperatures in the treatments with lower availability, which may be related to stomatal closure to prevent water loss to the environment. This result corroborates the analysis of *Physalis angulata* under abiotic stress conditions (Leite et al., 2018; Silva et al., 2021), in which plants subjected to water and salt stress, respectively, exhibited higher temperatures.

4.3. Biochemical aspects

The biochemical aspects of *P. angulata*, grown under water deficit, point to rapid changes in the physiological mechanisms for metabolic adjustments after the imposition of the deficit, for the content of proline (Figure 4b), total soluble sugars (Figure 4c) and reducing sugars (Figure 4d), however, the amino acid content was only influenced by water restriction in favor of regulating metabolic processes in the treatment with the greatest restriction on the fifth day of evaluation (Figure 4a), observing the interaction between WA and collection days.

When there was an interaction between the collection days and the WA levels (Table 3), it was observed that the amino acid content in the treatments with the highest restriction of 20 and 40% WA, showed the greatest significant accumulation on the fifth day of evaluation. However, the other treatments showed temporal variability in this process. For the other biomolecules evaluated, including total soluble sugars, reducing sugars, and proline in plants grown at 20% WA, the highest significant accumulation was observed on the fifth day of analysis, followed by a subsequent decrease on the following days. These aspects showed stability in the treatment with the highest water availability at 80% WA.

The biochemical changes triggered by stress, which can make plants tolerant to conditions that limit plant growth and development (Masouleh et al., 2019). The biochemical implications of water deficit are well documented, with the accumulation of organic solutes, proteins, sugars and amino acids (Santos et al., 2024; Silva et al., 2021; Lima, et al., 2024).

In *Physalis*, the accumulation of total soluble sugars, reducing sugars, sucrose, amino acids and proteins has been reported in different studies under conditions of abiotic interference (Leite et al., 2018; Silva et al., 2021; Lima et al., 2024), which may contribute to osmotic regulation (Santos et al., 2024).

According to Yang et al. (2021), soluble sugars can improve aspects of the plant's water status and can form hydrogen bonds with proteins to maintain the specific structures and functions of proteins. Under stress conditions, it is possible to observe an increase in the content of amino acids due to the degradation of proteins by proteases (Huang and Jander, 2017).

In addition, the accumulation of proline may result from an increase in the ratio between NADP + /NADPH, which will result in greater performance of the pentose phosphate oxidative pathway (Masouleh et al., 2019). Under stress conditions, proline can stimulate antioxidant enzyme activity, as well as binding to proteins to form a protective film, which prevents water loss (Yang et al., 2021).

The analysis of the main components on the fifth day of evaluation corroborates other studies on the imposition of water deficit, resulting in increases in biomolecules under conditions of water restriction, such as proteins, amino acids, soluble sugars, reducing sugars, sucrose, proline, leaf temperature and chlorophyll *a* and *b* (Leite et al., 2018; Silva et al., 2021; Lima et al., 2024; Santos et al., 2024).

The higher chlorophyll a (*Chl a*) and chlorophyll b (*Chl b*) indices (Figure 5) observed in *P. angulata* plants indicate a higher *Chl a*/*Chl b* ratio, reflecting metabolic adjustments required to cope with the period of water restriction (Yang et al., 2021). These results are consistent with previous studies on *Physalis* cultivation under water deficit conditions (Leite et al., 2018, 2021; Lima et al., 2024). This performance justifies the maintenance of photosynthetic activity in *P. agulata* (Figure 3 and Table 2) and the establishment of tolerance to water deficit. Drought stress can have an impact on the plant's photosynthetic apparatus, both in light-dependent and non-light-dependent reactions. In this sense, non-photochemical quenching (NPQ) mechanisms can help dissipate excess energy (Ruban and Wilson, 2020) and are important in protecting the photosystem during water stress (Qiao et al., 2024).

5. Conclusion

The performance of *Physalis angulata* is directly influenced by the period of exposure to water deficit and the levels of water availability, with changes in plant water status, gas exchange, biochemical aspects and chloroplastidic pigment indexes.

The period of exposure to water deficit of 5 days is recommended in studies on water deficit in *Physalis angulata*.

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Data Availability Statement

The data supporting the findings of the study "Water deficit exposure: physiological and biochemical changes in *Physalis angulata* L. (Solanaceae)" are available from the corresponding author upon reasonable request.

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