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RESEARCH ARTICLE

Effect of exogenous proline on the production and partitioning of dry matter and on the organic carbon content at different stages of the tomato plant

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Abstract

Water limitation is one of the most serious problems in tomato production, responsible for a significant reduction in productivity and fruit quality. In this context, the application of exogenous proline may be an alternative for plants to deal with possible water stress. The objective of this work was to evaluate the production, dry matter mass partition and organic carbon content of the tomato cultivar "Vivacy", cultivated with doses of proline and irrigated every seven days. A randomized block design was used, with four replications and a 2 x 3 + 1 factorial arrangement. The factors consisted of 2 doses of proline (100 and 150 mg L^{-1}), 3 application times (1, 3 and 6 days after irrigation) and a control without proline application. Data analysis showed a significant difference in the variables analyzed, revealing that the application of proline influenced the production and partition of dry matter mass of tomato plants. However, no significant difference was found in some variables, although the application of treatments showed superior results compared to the control. Proline sprayed at a dose of 100 mg L^{-1} increases the dry matter mass and organic carbon content in tomato plants during the fruiting and end-of-cycle phases, in addition to contributing to greater dry matter partitioning for the fruits.

Keywords: Vegetable; Amino acid; Compatible osmolytes; *Solanum lycopersicum* L; Water limitation.

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1. Introduction

In agriculture, the productivity of various crops, such as vegetables, can be affected by several factors including water limitation. Studies indicate that the reduction in water availability, driven mainly by climate change, will lead to major decreases in food production (Geilfus et al., 2024; Liu et al., 2025). In Brazil, the tomato plant (*Solanum lycopersicum* L.) stands out as one of the most consumed vegetables, with the largest producers being the states of Goiás, Minas Gerais, and São Paulo (IBGE, 2024). However, to achieve good yields, the crop is highly demanding in terms of water.

Water limitation is one of the most serious problems in tomato production, responsible for a significant reduction in productivity and fruit quality (Kuo et al., 2023). This stress factor directly alters plant physiology and influences photosynthesis, xylem and phloem transport, and the induction of sugar synthesis for osmotic adjustment, consequently affecting carbon allocation and partitioning (Aliche et al., 2020, Prabha et al., 2025). Plants use carbon in the process of photosynthesis, accumulating it as biomass in roots, leaves, stems, and fruits (Abdullah et al., 2021). Carbon content is considered a strong indicator of plant growth and development; however, it can be affected by various factors. The availability of light, water, and nutrients for the plant are the main factors influencing carbon acquisition and, consequently, biomass production (Irviring, 2015).

Given the problems of water limitation and, consequently, its influence on food production, it is essential to seek alternatives that contribute to the development and reproduction of plants. In this sense, the use of osmotically active solutes can favor cultivation even under water stress conditions. Proline is an amino acid commonly used to reduce the effects of water deficit stress. This solute plays a significant role in plant tolerance, enabling them to maintain turgor, as well as stomatal opening and gas exchange (Ojewumi et al., 2023; Sarker & Oba, 2018). Additionally, proline acts as an antioxidant, protecting the integrity of membranes and proteins (Khalid et al., 2022). Thus, its effect can enable plants to maintain growth rates even under adverse water conditions.

In a time when water deficit already limits agricultural production, the study of the influence of proline on the growth and development of tomato plants is of great importance to gain new insights for tomato cultivation. The analysis of production, partitioning of dry matter, and accumulated organic carbon in the plant can be useful for studying the crop's behavior under adverse environmental conditions.

Thus, the objective of this study was to evaluate the effect of proline sprays on production, partitioning of dry matter, and organic carbon content in tomato plants cultivated during the dry season and irrigated every seven days.

2. Methodology

2.1. Location of the experimental area

The experiment was conducted under field conditions from April to August 2022 at the Research, Teaching, and Extension Unit Horta Nova, of the Universidade Federal de Viçosa, located in Viçosa, Minas Gerais, Brazil. The study area was situated at the coordinates 20° 45′ 48" S and 49° 26′ 09" W, at an altitude of 666 m. According to the Köppen classification, the region's climate is Cwa (subtropical with dry winters). Figure 1 shows the data related to rainfall, minimum and maximum air temperatures, and relative humidity recorded during the experiment.

The soil in the experimental area is classified as Eutrophic Red-Yellow Argisol (Embrapa, 2018). Before the experiment was set up, soil samples were collected, and physical and chemical characterization was performed (Table 1).

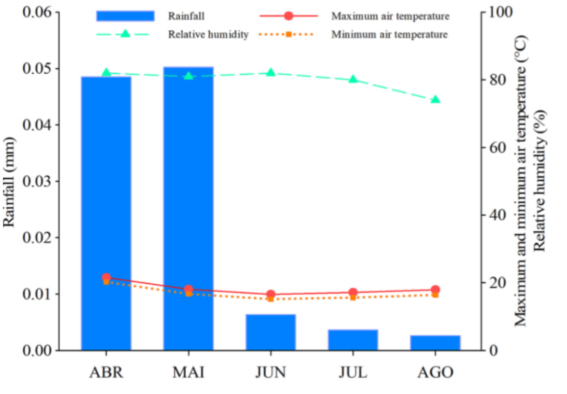

Figure 1. Climatic data from April to August 2022 in Viçosa, Minas Gerais, Brazil.

2.2. Soil Management, irrigation, and cultural practices

The area was prepared with plowing, harrowing, and subsoiling using 50 cm deep shanks. Gypsum application was carried out with 0.51 kg of gypsum per plot to prepare the soil profile and stimulate root growth in the plants. Phosphate fertilization was performed using Single Superphosphate, with 0.076 kg applied per planting hole, totaling 1.6 kg per plot on the surface and 1.6 kg per plot subsurface.

The remaining nutrient sources were applied through fertigation in a staggered manner throughout the crop cycle, following the recommendations of Alvarenga (2013). The fertilizers and quantities applied of urea, potassium chloride, calcium nitrate, magnesium sulfate, zinc sulfate, manganese sulfate, and boric acid were 952.7, 297.7, 297.7, 198.4, 21.8, 19.8, and 19.8 kg ha-1, respectively. The tomato seedlings of the cultivar Vivacy were produced in a commercial nursery using 128-cell polypropylene trays with a commercial substrate based on coconut fiber. Transplanting to the field was carried out with a spacing of 0.20 m between plants and 2.0 m between rows. The plants were trained using the Viçosa System (Almeida et al., 2015) for tomato cultivation, using twine and alternating inclination from one side to the other at 75° in relation to the ground. Weekly, suckering and pruning were performed, where the shoots that developed in the leaf axils and the terminal shoots of the stems were removed.

Table 1
Physical-chemical analysis of soil in the experimental area

Depth	Sand	Silt	Clay	P	K	Na	Ca	Mg	H+Al	Al	pH_{water}	MO
(cm)	-----------%-----------			-----mg/dm^3-----		----------cmol/dm^3--------						gag/kg^{-1}
0-20	34	18	48	29.5	132	3	3.7	1.1	4.2	0	5.8	2.9
20-40	28	19	53	9.3	67	3	2.9	0.78	2.9	0	5.4	1.8
40-60	21	19	60	1.8	39	4	2.7	0.77	2.9	0	5.6	1
60-80	30	29	41	1.2	31	3	2	0.64	1.3	0	5.8	0.4
80-100	18	24	58	1.6	34	3	2.5	0.71	1.6	0	5.8	0.8

pH in water: ratio 1:2.5. P, K and Na: Mehlich extractant 1. Ca, Mg and Al: KCl extractant 1 mol L^{-1}. H+AL: Calcium Acetate extractant 0.5 mol L^{-1} pH 7.0. MO (organic matter): Organic C. x 1.724 (Walkley-Black).

2.3. Experimental design and treatments

The experimental design used was randomized blocks in a 2 x 3 + 1 factorial arrangement, with four replications. The factors consisted of 2 doses of proline (100 and 150 mg L^{-1}), 3 application times (1, 3, and 6 days after irrigation), and a control without proline application (Figure 2). The experimental plots were 4.0 m wide and 1.2 m long, totaling 4.8 m^2, with three plant rows each. The central row of each plot was considered the useful area.

A localized drip irrigation system was installed, with emitters spaced 0.20 m apart and a flow rate of 2.1 L h^{-1}. The system's efficiency was evaluated by determining the Christiansen uniformity coefficient (Mantovani et al., 2013). Irrigation was carried out every seven days, as proposed by Fara et al. (2019). The total irrigation depth applied was 126.01 mm, calculated according to the methodology of Allen et al. (1998) based on the estimation of crop evapotranspiration. Foliar applications of proline were performed in the mornings using a backpack sprayer at three different times (30, 60 and 80 days after transplanting).

For sample preparation, tomato plants were collected and separated into stems, leaves, and fruits. The separated plant parts were washed with ultrapure water, placed in paper bags, labeled, and taken to a forced-air circulation oven at 65 °C until a constant mass was achieved. Subsequently, the parts were weighed and ground using a Willey-type mill equipped with a 20-mesh sieve.

2.4. Variables assessed

The evaluations of each characteristic were carried out at 80 and 120 days after transplanting, corresponding to the fruiting period and the end of the cycle, respectively. The dry matter mass of the samples was determined using a precision scale (0.01 g). To obtain the total dry matter mass, the sum of the plant parts was calculated. The value of 100% was assigned to the total production (all organs) of dry matter mass observed in the plants. Based on this reference value, the percentage production of dry matter for each plant organ was calculated according to the evaluation time, using the equation: Partition = (dry mass of the organ / total dry mass) x 100.

For the determination of organic carbon (%), the methodology proposed by Bezerra Neto & Barreto (2011) was used. To obtain the estimated productivity at each evaluation time (t ha^{-1}), the product of the fresh fruit mass harvested in each treatment and evaluation time by the plant population per hectare was considered.

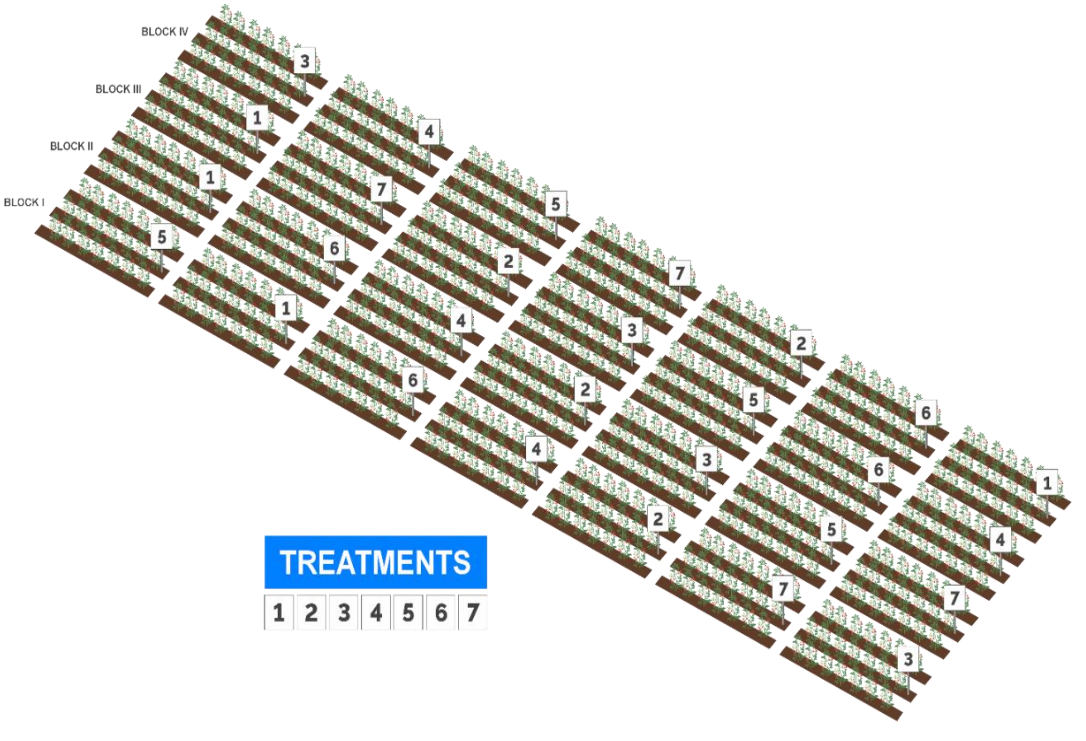

Figure 2. Scheme of the distribution of the experimental design. Treatments: 1: One day after irrigation at a dose of 100 mg L^{-1}; 2: Three days after irrigation at a dose of 100 mg L^{-1}; 3: Six days after irrigation at a dose of 100 mg L^{-1}; 4: One

day after irrigation at a dose of 150 mg L^{-1}; 5: Three days after irrigation at a dose of 150 mg L^{-1}; 6: Six days after irrigation at a dose of 150 mg L^{-1}; 7: Control.

2.5. Data analysis

The obtained data were tabulated and subjected to the Shapiro-Wilk normality test, analysis of variance, and, when significant effects were detected, Tukey's test ($p < 0.05$) was performed. To compare the means of the treatments with the mean of the control, Dunnett's test was used, adopting a 5% probability level. The RStudio software (Team, Boston, MA) and the ExpDes.pt package (Ferreira et al., 2014) were utilized. Logarithmic transformation was applied to the data of stem dry mass and organic carbon content at 120 days after transplanting.

3. Results and discussion

The dry matter mass of tomato leaves was influenced by proline spraying. At 80 days after transplanting, it was observed that the dose of 100 mg L^{-1} of exogenous proline contributed to a higher mass (75.6 g plant^{-1}) when applied six days after irrigation (Figure 3A). In contrast, at a proline dose of 150 mg L^{-1}, a greater increase was observed when applied one and three days after irrigation (Figure 3A).

Analyzing the application moments, it was observed that one and three days after irrigation, there was no difference between the applied proline doses. However, at six days, the proline sprayed at a dose of 100 mg L^{-1} resulted in a higher dry matter mass of leaves (Figure 3A).

At 120 days after transplanting, an increase in dry matter mass was observed compared to the control with doses of 150 and 100 mg L^{-1}, applied three and six days after irrigation, respectively (Figure 3B). Zouari et al. (2019) report that the osmotic adjustment promoted by proline application can enhance plant biomass under water stress. However, proline can have toxic effects if accumulated or applied at high concentrations, as excess proline may block its degradation in the catabolic pathway (Silao et al., 2023; Meena et al., 2019), which could explain better performance when a lower dose of the amino acid is applied. The effectiveness of the application depends on several factors, such as the applied dose, timing of application, and plant-related characteristics (Sharma et al., 2020).

The dry matter mass of stems was also influenced by the studied treatments. At 80 days after transplanting, the application of 100 mg L^{-1} of exogenous proline in tomato plants contributed to a higher accumulation of dry mass (68.8 g plant^{-1}) when applied six days after irrigation (Figure 4A). However, there was no significant difference in dry matter mass with application one day after irrigation (67.0 g plant^{-1}). At the dose of 150 mg L^{-1}, no difference was observed between application times.

When evaluating the influence of application timing, it was found that in both periods, the dose of 100 mg L^{-1} favored the production of stem dry matter mass (Figure 4A). At 120 DAT, the dose of 100 mg L^{-1} led to an increase in stem dry matter mass when applied six days after irrigation, reaching 99.1 g plant^{-1}. However, it did not differ significantly from the application one day after irrigation (Figure 4B). The dose of 150 mg L^{-1} showed no difference between application times.

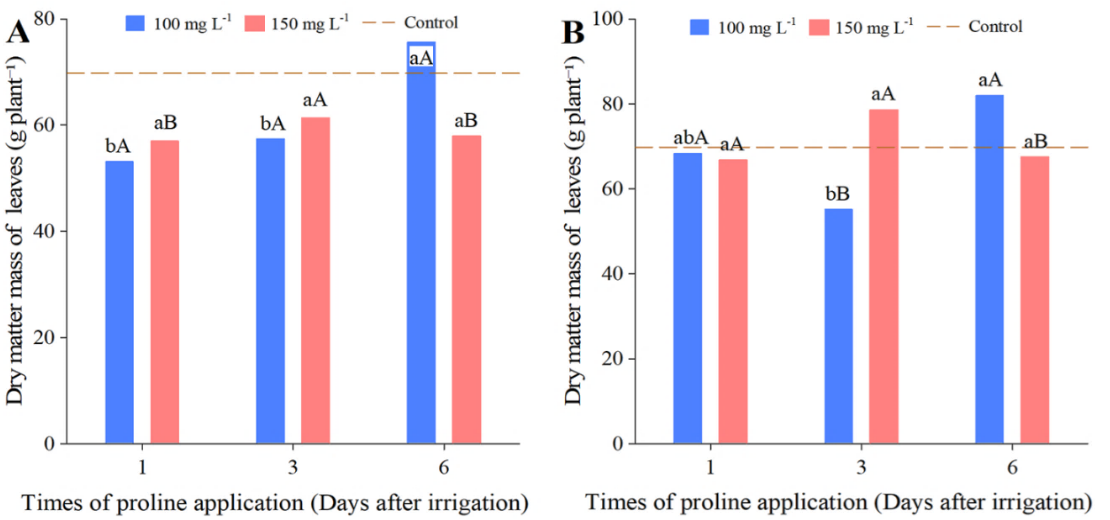

Figure 3. Dry matter mass of tomato leaves grown with different proline doses applied at three moments after irrigation, at 80 (A) and 120 (B) days after transplanting. Means followed by the same lowercase letters within the same proline dose and uppercase letters within the

same application time do not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

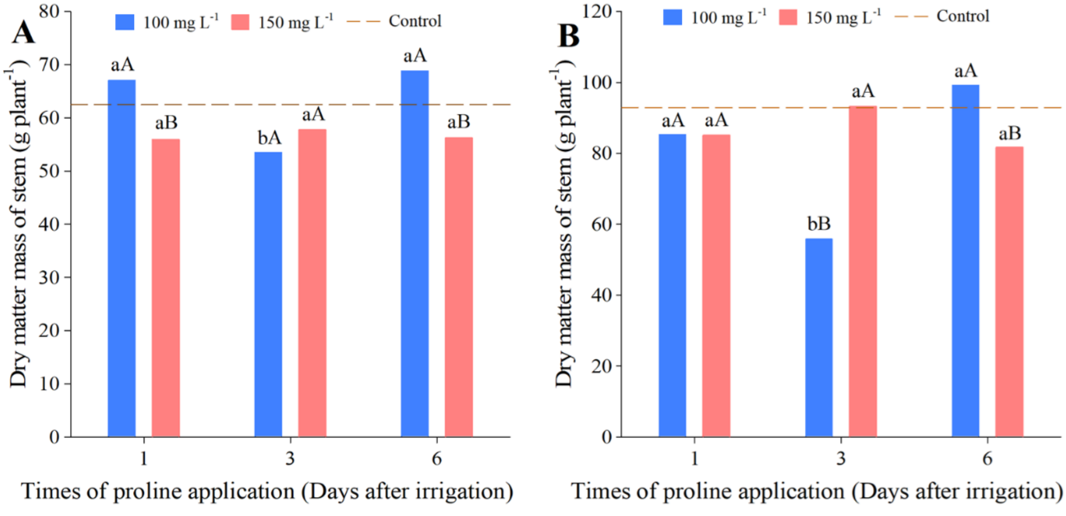

Figure 4. Dry matter mass of tomato stems grown with different proline doses applied at three moments after irrigation, at 80 (A) and 120 (B) days after transplanting. Means followed by the same lowercase letters within the same proline dose and uppercase letters within the same application time do not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

These results may be related to the ability of a specific dose at a given application time to promote osmotic adjustments without causing damage to the plant. Proline plays a protective role by maintaining cell turgor at an adequate level under stress, which influences the photosynthetic rate and plant growth (Renzetti et al., 2025).

In a study on foliar proline applications in bell pepper plants under salinity stress, Lima et al. (2016) observed that stem dry matter mass increased with proline application. However, they noted that the obtained mass decreased as the applied doses increased. On the other hand, Leite et al. (2022) found that proline could not mitigate the effects of water deficit on the stem dry matter of *Physalis peruviana*.

When evaluating the isolated effect of proline application timing on the dry matter mass of fruits in the Vivacy tomato cultivar at 120 DAT, it was observed that application one day after irrigation resulted in a 58.4% increase in dry matter mass compared to application six days after irrigation (Figure 5), with values of 222.8 g plant^{-1} and 140.6 g plant^{-1}, respectively.

According to Dawood et al. (2021), the responses to proline application are mainly determined by the timing of application and the concentration used. On the other hand, Gruszecki et al. (2022) described that the timing of proline application in relation to the plant's developmental stage may be more important than the amount applied. These findings also suggest that the effects of proline application on the plant are related to its developmental stage and/or the level of stress it is experiencing, consequently influencing dry matter mass.

It was observed that the exogenous application of proline at a dose of 150 mg L^{-1} influenced the dry matter partitioning in leaves (Figure 6A) at the end of the crop cycle. With this dose applied three days after irrigation, the plant allocated more dry matter to the vegetative part than in the other treatments, with a leaf dry matter percentage of 27.2%. This result was higher compared to the partitioning observed when applying 100 mg L^{-1} at the same timing (20%).

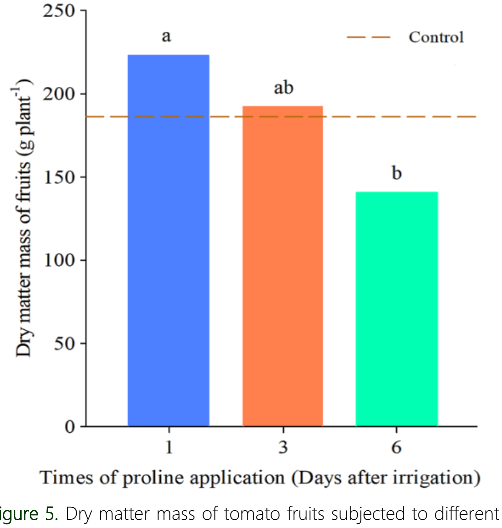

Figure 5. Dry matter mass of tomato fruits subjected to different proline application times after irrigation, at 120 days after transplanting. Means followed by the same lowercase letters do

not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

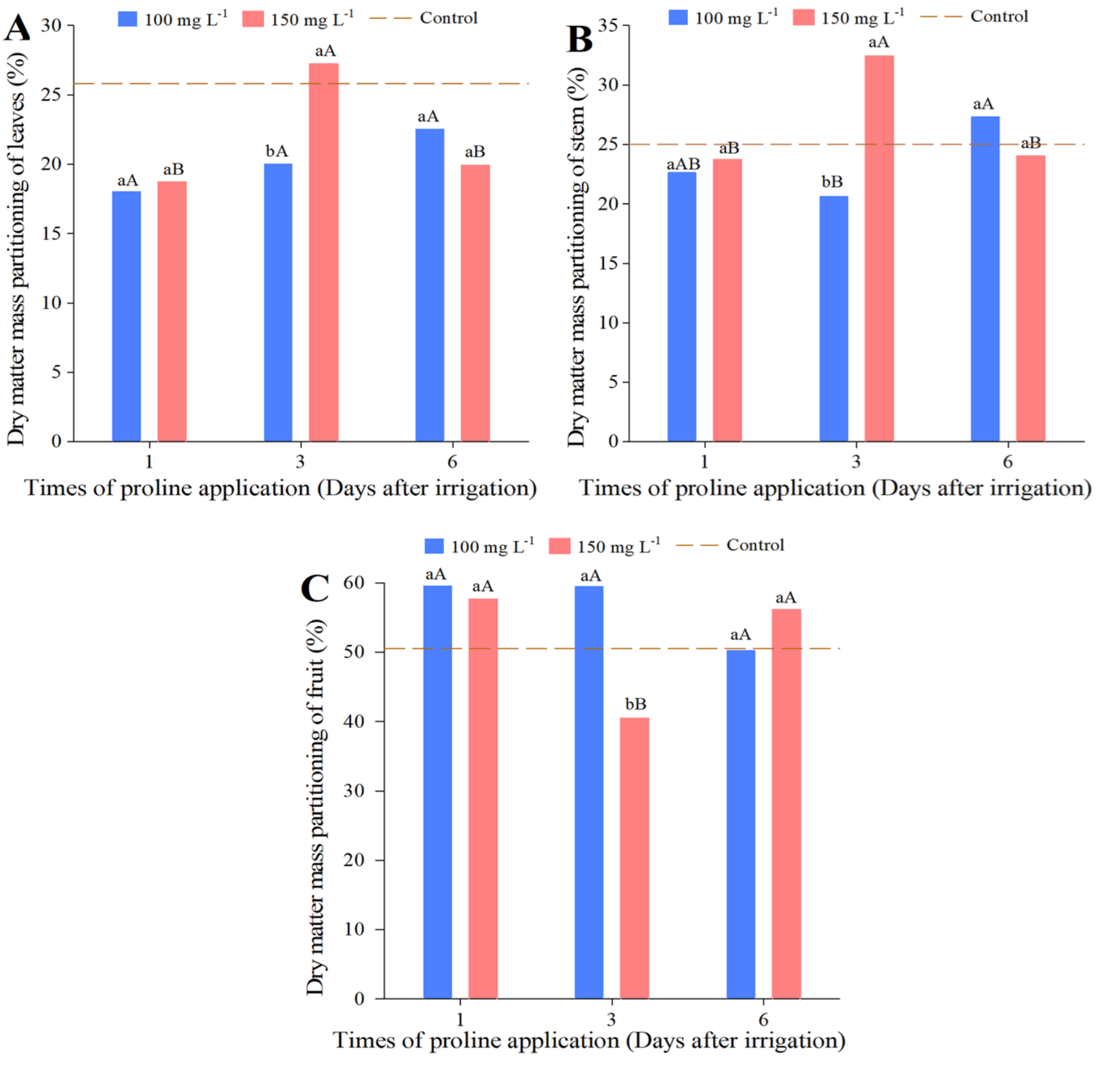

Figure 6. Partition (%) of the dry matter mass produced by Vivacy tomato plants into leaves (A), stems (B), and fruits (C) at 120 days after transplanting. Means followed by the same lowercase letters within the same proline dose and uppercase letters within the same application time do not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

Proline spraying can influence the allocation of biomass among plant organs, resulting in a redistribution of dry matter. This behavior is due to proline's ability to promote plant growth (Semida et al., 2020), which may lead to a greater allocation of dry matter to specific organs. Additionally, because of its role as an osmoregulator, proline can contribute to stomatal opening in plants under water limitation, leading to increased assimilate production, which in turn affects dry matter accumulation (Taiz et al., 2017).

When assessing dry matter partitioning in stems, similar results were observed. The application of 150 mg L^{-1} of proline three days after irrigation contributed to a greater allocation of photoassimilates to stems, with a partitioning percentage of 32.4%, compared to other treatments. Similarly, the application of 100 mg L^{-1} six days after irrigation also influenced partitioning, with 27.3% of dry matter allocated to stems (Figure 6B).

It is noteworthy that at this stage, leaves and stems typically receive considerably fewer assimilates than fruits, since, during the fruiting phase, assimilates are directed to this organ, which becomes the main sink. Thus, leaves and stems utilize assimilates primarily for structural maintenance of the plant (Martinazzo et al., 2015).

This behavior was observed in the dry matter partitioning of tomato fruits, where all treatments showed higher allocation compared to leaves and stems, indicating their role as the main sink. The highest fruit dry matter partitioning was observed with the application of 100 mg L^{-1} of proline at one and three days after irrigation, representing 59.5% and 59.4%, respectively (Figure 6C). Similarly to the results found in this study, Abreu et al. (2018), when evaluating the Caeté tomato cultivar, found that fruits were the primary sinks for photoassimilates, accounting for 48% of the dry matter mass.

Regarding organic carbon (C), at 80 days after transplanting, the application of 100 mg L^{-1} of exogenous proline three days after irrigation resulted in the highest carbon content in tomato leaves (17.7%) (Figure 7A). The dose of 150 mg L^{-1} showed no differences between application timings. When evaluating application timing, it was observed that in both periods, spraying with 100 mg L^{-1} of proline increased the organic carbon content in tomato leaves.

At 120 days after transplanting, the application of 100 mg L^{-1} of proline one day after irrigation contributed to a higher organic carbon content in leaves (22.5%) (Figure 7B). However, it did not differ significantly from the application three days after irrigation, which resulted in 19.3% organic C in the dry matter mass. When analyzing application timing, a higher organic C content was observed when proline was applied one day after irrigation. However, no differences were found between the studied doses during this period.

Water stress alters several physiological processes in plants, such as stomatal opening and closing, which consequently affect photosynthesis, respiration, and transpiration (Liang et al., 2020). Carbon content is influenced by various factors, including photosynthetic capacity, dry matter mass, and carbon metabolism. In this context, one of the main actions of proline as an osmoprotectant is mitigating the reduction in plant growth and photosynthetic activity under stress conditions (Altuntas et al., 2020). According to Cunha et al. (2022), the increase in organic carbon content due to the application of exogenous proline indicates that this amino acid helps maintain proper cell turgor, promoting CO_2 assimilation in accordance with stomatal conductance.

There is a scarcity of studies in the literature regarding the effects of amino acids, particularly proline, on organic carbon content in plants. In a scenario where higher food productivity is sought under water-limited conditions, determining carbon levels in plants is of great importance for conducting research and gaining new knowledge related to plant growth.

Regarding organic carbon content in tomato stems at 80 days after transplanting, an increase was observed with the application of 100 mg L^{-1} of proline three days after irrigation (Figure 8A), reaching 25.4%. However, this result did not differ significantly from the application one day after irrigation (23.9% organic C). The application of 150 mg L^{-1} of exogenous proline three days after irrigation also increased carbon content (24.4%). When evaluating application timing, it was observed that proline applied at a dose of 100 mg L^{-1} one and six days after irrigation was able to increase organic C content.

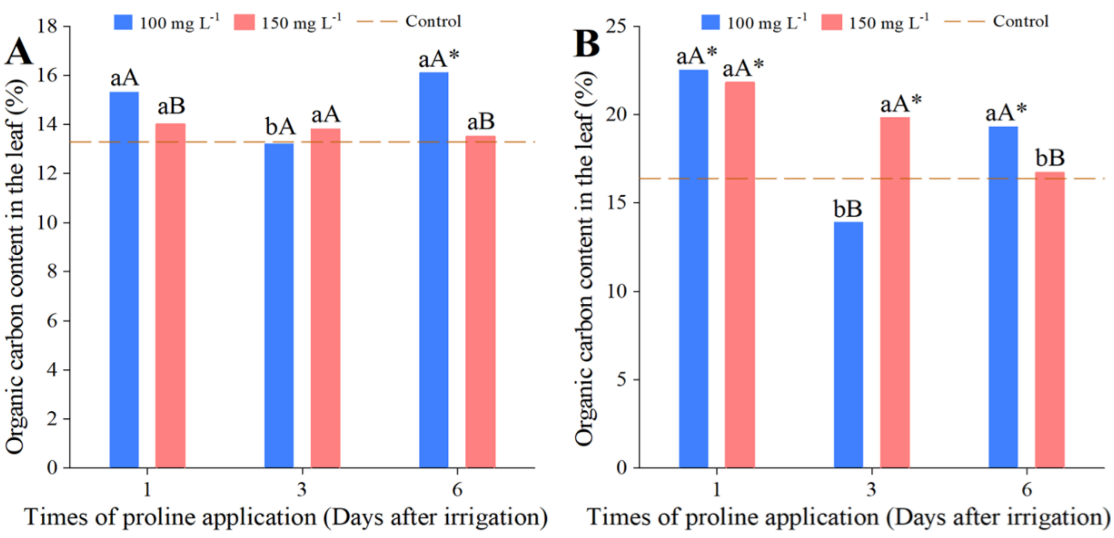

Figure 7. Organic carbon content in the leaves of Vivacy tomato plants subjected to different proline doses at different application times after irrigation, at 80 (A) and 120 (B) days after transplanting. Means followed by the same lowercase letters within the same proline dose and uppercase letters within the same application time do not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

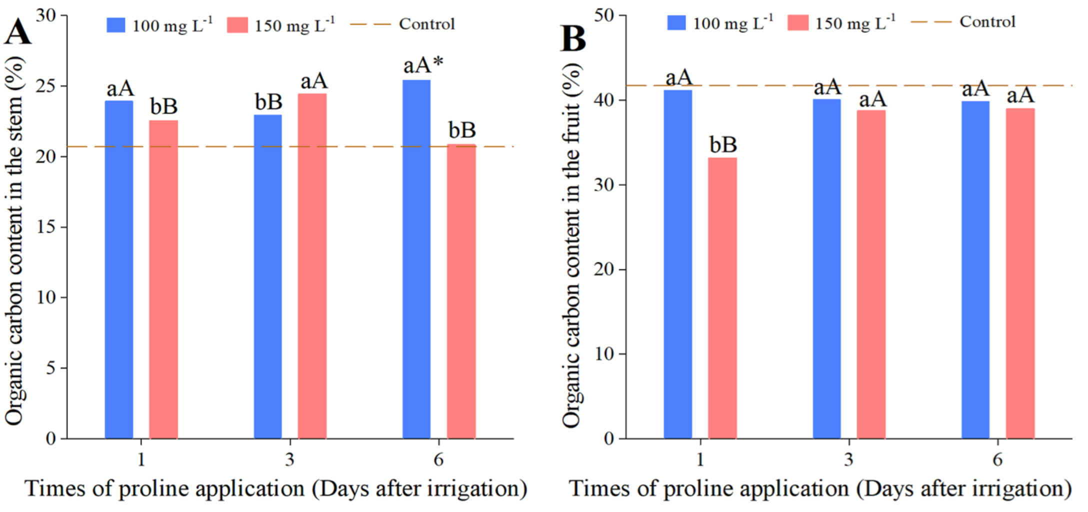

Figure 8. Organic carbon content in the stems (A) and fruits (B) of Vivacy tomato plants subjected to different proline doses at different application times after irrigation, at 80 days after transplanting. Means followed by the same lowercase letters within the same proline dose and uppercase letters within the same application time do not differ from each other according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

It is possible that the influence of proline on organic carbon content in stems occurs indirectly, as it primarily depends on plant-related factors, such as physiological and metabolic responses to the stress the plant is subjected to. During water deficit, stress can affect carbon metabolism, influencing its distribution and allocation. In this situation, it is feasible that proline acts as a carbon source (Taiz et al., 2017).

The effects of proline application on carbon metabolism have been reported by researchers. Tonhati et al. (2020) stated that exogenous proline contributed to higher carboxylation efficiency and photosynthetic pigments in tomato plants under heat stress. In a study on celery, Gao et al. (2023) found that proline accelerates the carbon assimilation pathway, enhancing the plant's photosynthetic efficiency.

Regarding carbon content in fruits at 80 days after transplanting, no significant differences were observed between the studied treatments and the control treatment (41.7%) (Figure 8B). However, it is noteworthy that the application of 100 mg L^{-1} of proline resulted in a higher organic carbon content one day after irrigation (41.1%), though it did not significantly differ from applications at three and six days after irrigation. Similar results were observed for the organic carbon content in leaves and stems.

When evaluating the isolated effect of proline doses at 120 days after transplanting, the highest organic carbon content in fruits was observed with the application of 100 mg L^{-1} of proline (Figure 9), reaching 50.2% organic C, followed by the 150 mg L^{-1} dose with 48.1%. However, this result was not significantly different from the control treatment (Figure 9).

Similar to dry matter mass, fruits exhibited the highest organic carbon content compared to other tomato plant organs. This behavior may be related to the fact that fruits store sugars, starch, and other carbon-rich components. Additionally, fruits can accumulate organic compounds that contribute to carbon content, such as phenolic compounds (Chaudhary et al., 2018).

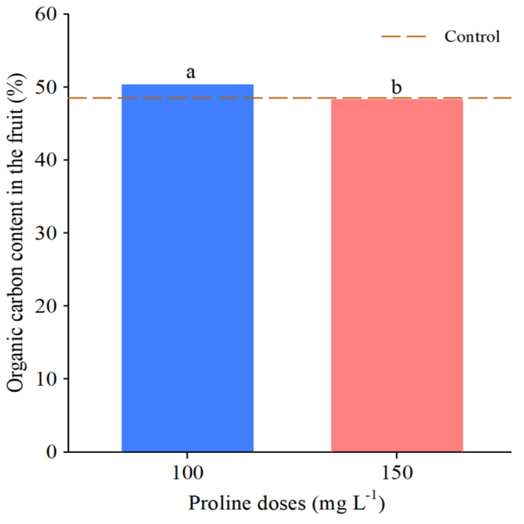

Figure 9. Organic carbon content in the fruits of Vivacy tomato plants subjected to different proline doses at 120 days after transplanting. Means followed by the same lowercase letters do not differ significantly according to Tukey's test ($p < 0.05$). Means followed by * indicate a significant result superior to the control treatment according to Dunnett's test ($p < 0.05$).

Considering the obtained results and findings in the literature, it is understood that the physiological stage of the plant should also be taken into account when applying proline (Dawood et al., 2021). In the present study, variability in plant performance was observed depending on proline doses and evaluation periods (80 and 120 days after transplanting), which correspond to the reproductive phase and the end of the harvest period, respectively. It is also worth noting that the duration of each phase depends on various factors, such as genotype, environment, and plant nutrition (Schmidt et al., 2017).

The estimated yield at each evaluation period was influenced by the timing of proline application at 120 days after transplanting. However, no significant difference was observed compared to the control treatment (Table 2). Among the application timings, proline spraying six days after irrigation contributed to higher yield, followed by application one day after irrigation.

Table 2
Estimated yield of Vivacy tomato at 80 and 120 days after transplanting

Times of proline application (after irrigation)	Estimated Productivity (t ha^{-1})	
	80 days after transplanting	120 days after transplanting
Control	22.41	63.07
1 day	18.71a*	69.18ab*
3 days	15.24a*	50.19b*
6 days	19.88a*	76.71a*

Means followed by the same letter in the column do not differ significantly according to Tukey's test ($p < 0.05$). Means followed by * indicate a non-significant result compared to the control treatment according to Dunnett's test ($p < 0.05$).

4. Conclusions

The effect of proline application on plants is related to their developmental stage and/or the level of stress they experience. Foliar application of proline at a concentration of 100 mg L^{-1} increases dry matter mass and organic carbon content in tomato plants subjected to water deficit during the fruiting and late growth stages. In the tomato cultivar Vivacy, applications of proline one or six days after irrigation contribute to greater dry matter accumulation. In the final stage of the crop cycle, proline at a dose of 100 mg L^{-1} promotes greater dry matter partitioning to the fruits. Lower doses and new horticultural crops are suggested for future studies. The evaluated indicators are promising for advancing research on food production in adverse environmental conditions, especially in the face of climate emergencies.

Author contribution

J. Oliveira, R. I. Corella, D. L. Nascimento, M. S. Barbosa, D. J. H. Silva, H. E. P. Martinez: Conceptualization, Developmentor design of methodology and Data collection. **J. Oliveira, R. I. Corella, D. L. Nascimento, M. S. Barbosa:** Data analysis & interpretation. **J. Oliveira, D. J. H. Silva, H. E. P. Martinez:** Writing, editing & text reviewer.

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