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Gas Exchange in Tomato under Different Water Management in Cultivation

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Abstract

The water management in the tomato crop has a direct effect on the development and yield, however the gas exchange rates of the plant can be influenced by the management and evaluation period. The study aimed to analyze gas exchange in tomato, in full production, in plants cultivated under different water management. The experiment was conducted in a completely randomized design with two water conditions during cultivation (with deficit and without deficit). The management of the water deficit adopted using different depths of water replacement, under water deficit the replacement of 60% of the crop evapotranspiration (ETc) was carried out while in the condition without deficit there was replacement of 100% of the ETc. The determination of gas exchanges, in a period with full production, was performed at 70 and 71 days after transplanting, determining photosynthesis (A), stomatal conductance (Gs), internal CO_2 (Ci) and transpiration (E). From the A/E ratio, the intrinsic water use efficiency (iWUE) was calculated. The data were submitted to analysis of variances and the means compared by the Tukey test with 5% of significance. There is significant variation in gas exchange rates depending on the water management adopted and evaluation period. Water deficit has a cumulative effect on plants. Tomato plants cultivated with water deficit (60% of ETc) have lower rates of gas exchange, with no full recovery of rates even after irrigation. Tomato plants grown without water deficit (100% of ETc) show adaptation and compensation in gas exchange due to soil drying.

Keywords: plant physiology, water management, *Solanum lycopersicum* L.

1. Introduction

The tomato (*Solanum lycopersicum* L.) originates from South America, currently being produced on different continents, and presenting a significant cultivation area and economic return, among vegetable species (Brandão-Filho). The development and yield of the crop is associated with genetic, environmental and management factors, with emphasis on water availability during the cycle (Zhou et al., 2020; Cao et al., 2020). In relation to water management, both deficit and excess conditions can harm flowering and fruiting, consequently impacting crop yield (Silva et al., 2020).

Water is a relevant factor for plant production, with most plant transpiration dependent on water from short-term rainfall (Miguez-Macho; Fan, 2021), which is limiting in dry crops. Soil water storage is influenced by physical-hydric factors, showing temporal persistence over time (Hara et al., 2020), in the absence of actions that drastically alter its properties. While water stress may pose challenges to crop productivity, it paradoxically serves as a catalyst for enhancing the resistance and adaptability of plants (Liu et al., 2016). The intricate relationship between the photosynthetic mechanism and crop yield is widely acknowledged in the scientific literature (Zhang et al., 2018; Fang et al., 2018). In response to water stress, crops employ a spectrum of physiological processes, encompassing the regulation of stomata, photosynthetic rapid reaction, and the activation of antioxidant defense mechanisms (Li et al., 2017). These intricate mechanisms, while mitigating the potential negative impacts on yield, underscore the adaptive strategies employed by crops to thrive in the face of challenging environmental conditions. Regarding soil water balance, there are several mathematical models applied to determine water inputs and outputs in the system, helping with irrigation planning and allowing efficient use of resources (Pereira; Paredes; Jovanovic, 2020).

The irrigation technique allows an increase in the productive potential, based on the supply of water in adequate periods and considering characteristics of the soil, plant, method and production system (Santos; Vanzela; Faria, 2018). Methods based on meteorological data (Allen et al., 1998), lysimetry (Vellame et al., 2012), tensiometry (Mourelli, 2008), and sensors (Pereira; Paredes; Jovanovic, 2020) are used to determine the volume of replacement water. , with water replacement adjusted to the method employed and management adopted.

The presence of water deficit in plant development is a naturally avoided condition, especially in irrigated agriculture. However, the existence of reduced water availability in the soil for plants occurs naturally and temporarily, related to soil drying between irrigations (Ishfaq et al., 2020), and in an induced way when performing water management with controlled deficit, aiming to increase the efficiency of resource use (Terassi et al., 2021, Saath et al., 2022). Normally, the plant response to different water conditions during development is based on crop yield, with the assessment of gas exchanges analyzed only occasionally, when evaluated. Considering the influence of gas exchange on plant development, the study aimed to analyze gas exchange in tomato, in full production, in plants cultivated under different water management.

2. Method

The study was conducted in a protected environment at the Technical Irrigation Center (CTI) of the State University of Maringá (UEM), Maringá, Brazil (23º25'57" S, 51º57'08" W and 542 m altitude). The experiment was conducted in a completely randomized design with two water conditions during cultivation (deficit and without deficit). The management of the water deficit adopted using different depths of water replacement, under water deficit the replacement of 60% of the crop evapotranspiration (ETc) was carried out while in the condition without deficit there was replacement of 100% of the ETc.

Tomato cultivation was carried out in beds (3 m long, 1 m wide, and 0.5 m high). Commercial seedlings (Graziani hybrid, SAKATA Seeds, Brazil) were implanted with a spacing of 0.75 m between plants. The plants, with an indeterminate growth habit, were conducted with two stems and in a tutored manner up to a height of 2 m from the soil surface.

The soil in the beds is characterized as Nitossolo Vermelho distroférrico according to the Brazilian Soil Classification correlated with Utissol in the Soil Taxnomy Classification (Santos et al., 2018). As physical, parameters, the soil has a very clayey texture (72% of clay, 16% of silt, 7% of fine sand, and 5% of coarse sand), and a bulk density of 1.1 Mg m^{-3}. As a chemical parameter (0 – 0.2 m soil layer), it presented pH (CaCl2): 6.30, organic matter: 1.99%, phosphorus: 84.01 mg dm^{-3}; potassium: 0.46 cmol dm^{-3}; calcium: 7.62 cmolc dm^{-3}; magnesium: 1.80 cmolc dm^{-3}; copper: 15.24 mg dm^{-3}; iron: 55.86 mg dm^{-3}; manganese: 127.98 mg dm^{-3}; zinc: 9.0 mg dm^{-3}.

Before transplanting, the soil was fertilized with 150 kg ha^{-1} of N (urea, Mosaic® Fertilizantes do Brasil, Paranaguá, PR, Brazil), 131 kg ha^{-1} of P (single superphosphate, Mosaic® Fertilizantes do Brasil, Paranaguá, PR, Brazil), 150 kg ha^{-1} of K (potassium chloride, Mosaic® Fertilizantes do Brasil, Paranaguá, PR, Brazil), and 4 kg ha^{-1} of B (boric acid, Fertilizantes Heringer®, Paulínia, SP, Brazil), considering the recommendations for crop (Pauletti; Motta, 2019).

To determine the daily evapotranspiration of the crop, constant-level water table lysimeters were used, as described by Andrean et al. (2022). In the lysimeters, tomato plants were cultivated with management and spacing similar to that adopted in the beds. The determination of evapotranspiration was determined daily (7 a.m.) by the difference in water volume.

To determine the moment of irrigation, tensiometers installed at 5 and 15 cm deep were used (Figure 1), with daily (8 a.m.) readings of the matrix tension with a digital manometer. The critical stress adopted was -30 kPa, as recommended by Mourelli (2008) for the crop and irrigation method employed.

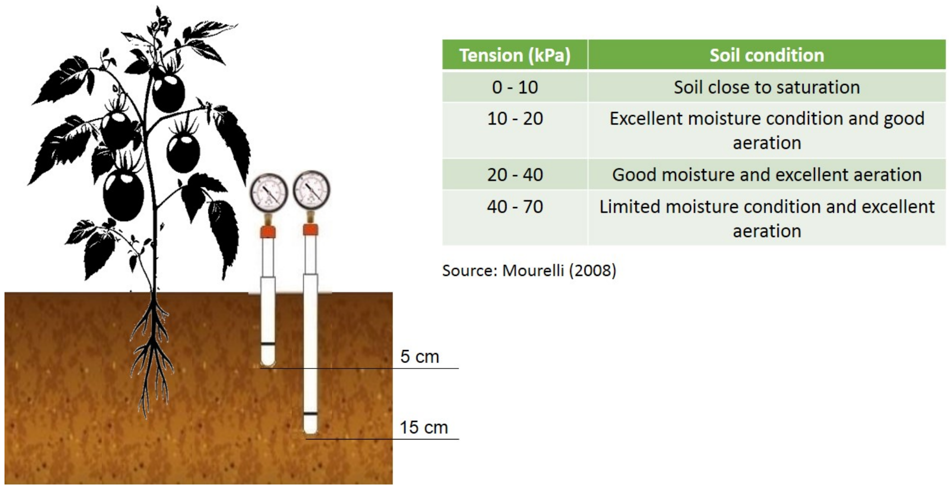

Figure 1. Diagram of tensiometer batteries

To define the critical moment, the readings obtained in the beds with 100% ETc replacement were considered, with water replacement being carried out in all conditions with variable volume with the respective treatment (60 or 100% of ETc). Water replacement was performed with self-compensating drippers with a nominal flow of 4 L h-1, with spacing of 0.3 m and Christiassen uniformity coefficient (CUC) of 94%.

The determination of gas exchanges was performed at 70 (before irrigation) and 71 (after irrigation) days after transplanting, in the period from 8 a.m. at 10 a.m. The equipment LI-6400XT Portable Photosynthesis System (Li-COR, United States of America) was used, being adopted as configuration: flow rate = 500 µmol s^{-1}, Photosynthetic Photon Flux Density (PPFD) = 1500 µmol m^2 s^{-1}, Mixer reference CO_2 = 400 µmol mol^{-1}, at room temperature. Photosynthetic rate (A, µmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapour (Gs, mol m^{-2} s^{-1}), internal CO_2 rate (Ci, mmol m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}), intrinsic water use efficiency (iWUE, mmol CO_2 mol^{-1} H_2O) which is the A/E ratio, were evaluated.

Data were subjected to analysis of variance, and the effect of isolated factors and interaction was verified. Means were compared using the Tukey test with 5% significance, considering the sources of variation. The linear correlation between the variables in each cultivation condition and evaluation period was determined. For data analysis, MS Excel and SISVAR software (Ferreira, 2019) were used.

3. Results and Discussion

Considering the water management adopted (with or without water deficit) and the evaluation period (before or after irrigation) as a source of variation, the effect on the variables analyzed was verified, with the summary of the analysis of variance shown in Table 1.

Table 1. Summary of analysis of variance

Source of variation	A (µmol CO_2 m^{-2} s^{-1})	Gs (mol m^{-2} s^{-1})	Ci (mmol m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	iWUE (mmol CO_2 mol^{-1} H_2O)
Water management (W)	*	*	**	***	**
Evaluation period (E)	***	***	***	**	***
W x E	*	ns	ns	ns	ns
Mean	9.08	0.028	282.68	1.53	5.35
Coefficient of variation (%)	8.96	13.36	26.58	29.79	13.17

*: $p < 0.01$; **: $p < 0.05$; ***: $p < 0.1$; ns: non significant ($p > 0.1$); A: photosynthetic rate; Gs: stomatal conductance; Ci: internal CO_2; E: transpiration; iWUE: intrinsic water use efficiency.

According to Hara et al. (2020), in assessments at the study site, verified temporal persistence in the soil water storage characteristic, implying that the differences observed in the study do not originate from spatial variability. The imposition of water deficit in the development of the crop, causes negative rates in the water balance with a cumulative effect over time, resulting in differences in water tension in the soil obtained in the evaluation periods, with variation in tension after irrigation of 11, 25 kPa (Figure 2), between condition with deficit (60% of ETc) in relation to condition without deficit (100% of ETc).

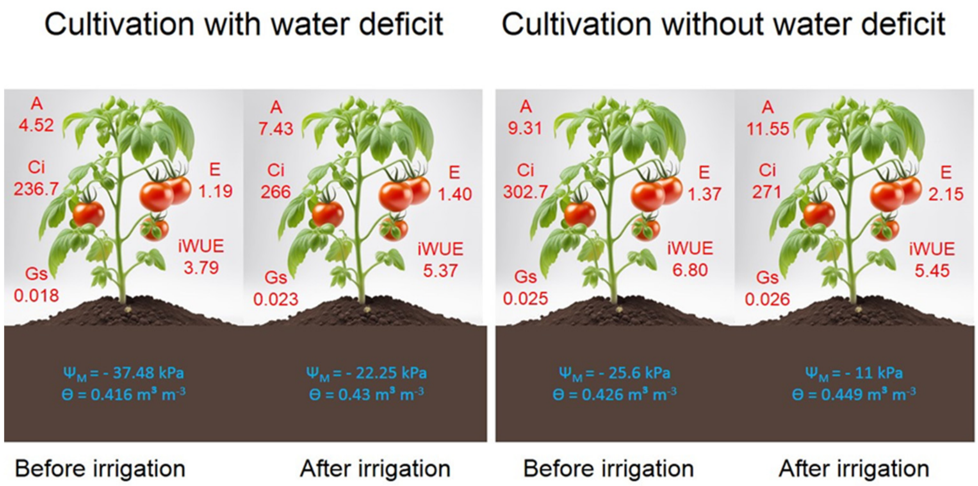

Figure 2. Gas exchange rates in tomato plants cultivated with different water management, before and after irrigation

According to the mathematical model of the soil water retention curve of the experimental area (θ=0.5199x-0.0611), proposed by Trintinalha (2005), the variation of water tension in soil after irrigation indicates a difference in humidity of 0.019 m^3 m^{-3} (Figure 2). This condition indicates that even after irrigation, the condition of cultivation with water deficit (60% ETc) does not present moisture close to saturation, with levels close to those reported by Mourelli (2008) as a critical limit for irrigation. This fact is the result of the cumulative effect of the imposition of the water deficit mentioned above, in which the water balance is negative, with the outputs being greater than the water input into the production system.

The condition of imposition of water deficit (60% of ETc) causes unfavorable water conditions throughout the development of the tomato plant, requiring adaptations to maintain the water potential of the plant. In dry soil conditions, there are chemical and physical responses to preserve the water potential of plants. Chemical responses are related to increased synthesis and transport of abscisic acid, rapid signaling and stomatal closure, while physical responses are associated with root development and hydraulic conductivity of cells (Ishfaq et al., 2020).

As obtained in the study, photosynthesis rates are reduced as a result of soil drying, being lower in conditions of cultivation with water deficit (60% of ETc), as shown in Table 2. The results of the studies corroborate Liang et al. (2019) who obtained a reduction in the net photosynthesis rate as a function of soil moisture.

Table 2. Photosynthetic rate (A), stomatal conductance (Gs), internal CO_2 rate (Ci), transpiration (E), intrinsic water-use efficiency (iWUE) in tomato under different conditions and evaluation periods

Water condition	Evaluation period	A (μmol CO_2 m^{-2} s^{-1})	Gs (mol m^{-2} s^{-1})	Ci (mmol m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	iWUE (mmol CO_2 mol^{-1} H_2O)
With deficit	Before irrigation	4.52 bB	0.018 bB	236.7 bB	1.19 bB	3.79 bB
Without deficit		9.31 aB	0.025 aA	302.7 aA	1.37 aB	6.80 aA
With deficit	After irrigation	7.43 bA	0.023 aA	266 aA	1.40 bA	5.37 aA
Without deficit		11.55 aA	0.026 aA	271 aB	2.15 aA	5.45 aB

*Different letters in the column, lowercase for water condition and uppercase for evaluation period, indicate a significant difference by the Tukey test with 5% significance.

As a plant response to maintaining water potential under conditions of water stress, there is a rapid response in transpiration, which is reduced due to stomatal closure. In the study, the difference between the transpiration rate of the cropping condition with deficit (60% of ETc) and without deficit (100% of ETc) is 13.13 and 34.88%, before and after irrigation, respectively (Table 2). Although, reducing transpiration can result in water savings for the plant and greater intrinsic water-use efficiency (Table 2), the relationships between the variables (photosynthetic rate, stomatal conductance, internal CO_2 rate, and transpiration) and the consequences for the plant must be considered.

Wenneck et al. (2023b), when analyzing morphological issues, yield, commercial quality and yield of cauliflower (*Brassica oleracea* var. *botrytis*) cultivated with different water management, concluded that the imposition of a moderate deficit in cultivation can lead to improvements in commercial characteristics and water use efficiency, but there is a decline in income and economic return. Therefore, in addition to development and yield parameters, different factors related to production must be considered.

According to Zhou et al. (2020) maintenance of the transpiration rate is essential for ecophysiological processes in tomato, and is also influenced by nutritional issues, and the flow of water from the soil to the plant contributes to the absorption of elements by mass flow. Furthermore, it should be considered that transpiration is related to morphological characteristics, mainly leaf area, size and density of stomata (Jo; Shin, 2021).

Tomato plants cultivated with water deficit (60% of ETc) have a lower stomatal conductance rate even after irrigation (Table 2). This result is similar to that obtained by Hernandez-Espinoza and Barrios-Masias (2020), resulting from changes in root anatomy and hydraulic conductance. According to Harrison et al. (2019) plants need to raise internal CO_2 rates for photosynthesis, and under adverse conditions, such as water stress, they maximize stomatal conductance. However, the increase in stomatal conductance also changes the transpiration rate, requiring regulation to increase the intrinsic water-use efficiency (iWUE).

Based on the data obtained in each condition and period, a linear correlation analysis was performed between the analyzed variables (photosynthesis - A, internal CO_2 - Ci, stomatal conductance - Gs, transpiration - E, intrinsic water‑use efficiency - iWUE), with the bivariate correlation classified as very weak |0 - 0.19|, weak |0.2 – 0.39|, moderate |0.4 – 0.69|, strong |0.7 – 0.89| and very strong |0.9 – 1|, as shown in Figure 3.

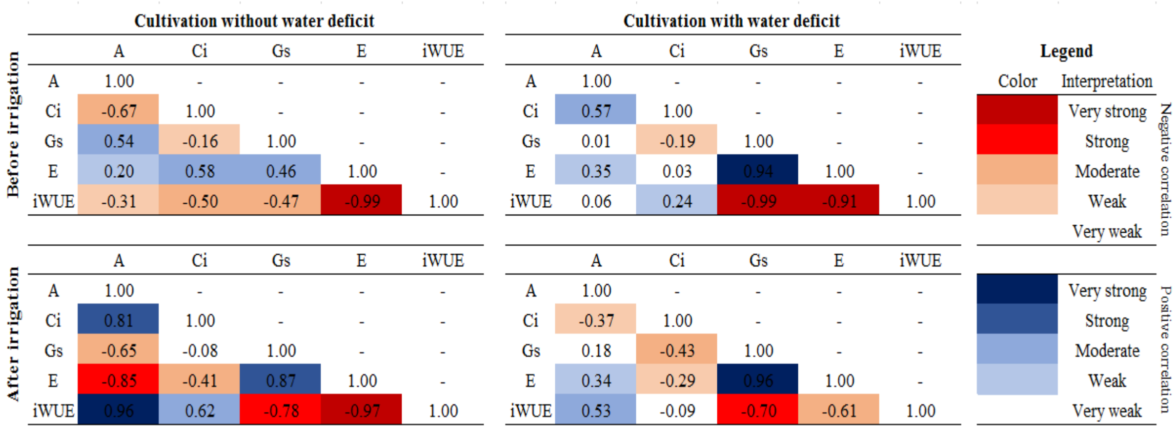

Figure 3. Correlation of variables (photosynthesis - A, internal CO_2 - Ci, stomatal conductance - Gs, transpiration - E, intrinsic water-use efficiency – iWUE) for different cultivation conditions and evaluation period

The correlation between intrinsic water‑use efficiency (iWUE) and transpiration (E) ranges from moderate to very strong, with an inverse trend (Figure 3). While the correlation between stomatal conductance (Gs) and transpiration (E) is positive from moderate to strong in all conditions and periods analyzed. These data highlight the complexity associated with the interaction between physiological parameters when changing cultivation conditions, as addressed with water management and the evaluation period in this study.

The highest rate of intrinsic water-use efficiency (iWUE) was obtained in cultivated plants without water deficit in the period prior to irrigation (Table 2). In this condition, although transpiration showed a high rate, an increase in stomatal conductance and CO_2 rates was also verified, resulting in a higher rate of photosynthesis. This result corroborates the adaptation relationship presented by Harrison et al. (2019) and cited earlier.

Tomato plants cultivated with water deficit (60% of ETc) have low intrinsic water-use efficiency (iWUE) in the period prior to irrigation, being close to the condition without deficit after irrigation (Table 2). The difference in intrinsic water - use efficiency (iWUE) before irrigation as a function of water conditions (60 and 100% of ETc) in cultivation is possibly related to the cumulative effects of drought stress, which involve morphological development, nutrition, osmotic regulation, cell turgor, membrane integrity, damage to the photosynthetic apparatus, hormonal balance, in addition to several factors with a direct and indirect impact (Yang et al., 2020; Mushtaq et al., 2022).

The study conducted by Hao et al. (2019), investigating the physiological responses of tomato to water stress and re-water in different growth periods, concluded that the impact of water stress on photosynthetic rate and stomatal conductance during anthesis was significantly greater compared to the other two growth periods, even when subjected to the same degree of water stress. There was a substantial reduction in the values of photosynthetic rate and stomatal conductance during this critical stage, which, following re-water, did not return to the levels observed in the control group. The primary reason for this phenomenon lies in the fact that the anthesis phase is crucial, and inadequate irrigation during this period fails to adequately meet the physiological needs of tomatoes (Alou et al. 2018).

Although studies with controlled water deficit demonstrate productive persistence in terms of yield at some stress-induced levels (Terassi et al., 2021; Saath et al., 2022), it must be considered that water management is capable of altering quality as well (Mediyouni et al., 2021) and the final composition of vegetables (Soares-Wenneck et al., 2023). In this sense, associated practices are necessary to mitigate the effect of water stress on tomato quality and yield (Abdallah, 2019; Zhang et al., 2021) and improvement in gas exchange (Wenneck et al., 2023a).

4. Conclusion

There is significant variation in gas exchange rates depending on the water management adopted and evaluation period.

Water deficit has a cumulative effect on plants. Tomato plants cultivated with water deficit (60% of ETc) have lower rates of gas exchange, with no full recovery of rates even after irrigation.

Tomato plants grown without water deficit (100% of ETc) show adaptation and compensation in gas exchange due to soil drying.

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Authors contributions

Conceptual idea: GSW, RS, and RR; Methodology design: GSW, RS, RR, and ALM; Data collection: GSW, LHMS, DST, ALM, and AFBAA; Data analysis and interpretation: GSW, RS, and DST; Writing and editing: GSW, and DST; Supervision: RS and RR.

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The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Data sharing statement

No additional data are available.