



## Research article

## Identification of water stress in tomato based on spectral indices and physiological parameters

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### Abstract

**Importance of the work:** Generally, farmers use a large amount of water to produce greenhouse cherry tomatoes, resulting in increased production costs and possibly suboptimal excessive water use.

**Objectives:** To investigate the optimum water content for ‘Sweet Boy’ cherry tomato production, based on changes in tomato physiology and yield.

**Materials and Methods:** A completely randomized design was used, consisting of four levels of pot water capacity (PC; 60%PC, 80%PC, 100%PC (the control) and 120%PC) as the water-holding level in the growing medium. Physiological responses and tomato yield in each treatment were measured.

**Results:** Water levels of 60%PC and 80%PC decreased the tested spectral indices (the normalized difference vegetation index, the normalized difference red-edge index and the photochemical reflectance index). Furthermore, a water content of 60%PC significantly reduced the net photosynthetic rate (22.63–32.08%) and stomatal conductance (57.23–88.29%) in the vegetative and flowering stages compared to 100%PC. In addition, 100%PC achieved similar physiological and yield responses as 120%PC. After fruit harvest, 60%PC and 80%PC reduced the fruit weight and the total yield per plant. However, 60%PC produced significantly higher total soluble solids (9.48°Brix), ascorbic acid (9.11 mg/kg fresh weight, FW) and lycopene (4.24 mg/kg FW) contents than the control.

**Main finding:** Irrigation at 100%PC and 120%PC produced similar physiological responses and yields in cherry tomato plants. Therefore, 100%PC irrigation reduced water use by 32% compared to the 120%PC treatment while maintaining high yield and acceptable fruit quality. It is recommended that farmers irrigate at 100%PC to optimize productivity and efficient water use.

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## Introduction

Tomato (*Solanum lycopersicum* L.) is one of the vegetables widely consumed fresh or processed and is a vegetable crop cultivated in greenhouses (Du et al., 2017). The tomato fruit contains high nutritional value, providing a source of antioxidants, fiber, vitamins, potassium, phenolic compounds, lycopene and  $\beta$ -carotene (Dumas et al., 2003) in the human diet, which have been linked with reduced risk of cancer and heart diseases (Clinton, 1998). Among the tomato group, cherry tomato is one of the popular types because it contains high levels of total soluble solids and volatile organic compounds that contribute to its tastiness and pleasant smell (Beckles, 2012; Liu et al., 2018).

Feeding the increasing global population requires greater harvested volumes of food crops and consequently more water use. It is estimated that the world's water use for crop production is 6,800 km<sup>3</sup> per year and increasing rapidly (Mialyk et al., 2024). Tomato productivity and quality are highly dependent on precise water management (Santana and Vieira, 2010). Reducing water wastage and supporting the transformation of water and food systems under climate change requires managed irrigation by applying the appropriate amounts of water at the right time, depending on the specific crop type (Smith et al., 2023). Tomato plants have a high water-use rate because they have a high transpiration rate (Cantero-Navarro et al., 2016). In the complete tomato life cycle, the plants have maximum water demand during flowering and fruit growth (Hott et al., 2018). To ensure that cherry tomatoes receive sufficient water, farmers usually supply excess water in the growing medium, for example, 140% of crop evapotranspiration ( $ET_c$ ) has been recommended for farmers (Colimba-Limaico et al., 2022), which might increase the cost of tomato production and result in suboptimal water use. Irrigation management based on physiological stages could serve as a tool to address both of these issues.

Irrigation is an important agricultural management method for improving the quality and yield of tomato fruits, while reducing the pressure on the environment caused by horticultural production (Li et al., 2021a) and also saving water (Li et al., 2021b). The water volume can affect the water absorption of plant roots by changing the water content, temperature and nutrients in the rhizosphere environment (Steudle, 2000). Crop water requirements are primarily estimated using reference crop evapotranspiration

( $ET_0$ ) (Hadi et al., 2017),  $ET_c$  (Harmanto et al., 2005; Colimba-Limaico et al., 2022) and field capacity (Zhang et al., 2021). However, with pot planting, the water consumed could be considered as the pot water capacity, referring to the amount of water remaining in a pot after watering and visible drainage has finished (Kirkham, 2005). Water stress causes a drop in photosynthetic activity, which reduces the growth and development of crops (Dangwal et al., 2016). The amount of water required by vegetables depends on the plant species, cultivar and growth conditions (Nemeskéri and Helyes, 2019). A study of the bell pepper, belonging to the family Solanaceae (as does the tomato), reported that a deficit irrigation level at 67%  $ET_c$  reduced plant growth and leaf gas exchange but did not alter fruit yield and quality (Kabir et al., 2021). Nahar and Gretzmacher (2002) reported that the tomato cultivars BR-1, BR-2, BR-4 and BR-5 grown at a water content of 70% field capacity (FC) produced a higher fruit fresh weight per plant than those grown at 100%FC and 40%FC. In addition, the optimum irrigation level for the cherry tomato 'Troy 489' grown in the greenhouse was approximately 75–100%  $ET_c$ , as plants grown within this irrigation range produced a higher marketable yield than those irrigated at 25–50%  $ET_c$  (Harmanto et al., 2005). Thus this evidence suggests that supplying a high amount of water does not always benefit plant production.

Recent advancements have focused on non-destructive and real-time monitoring of plant water status to enhance irrigation precision. For example, the use of remote sensing and spectral vegetation indices has provided a sophisticated approach to detecting water stress in greenhouse vegetables before visible symptoms appear, thereby enabling more timely and efficient irrigation management (Ihuoma and Madramootoo, 2019a; 2019b). The reason for using these techniques becomes stronger when considering the mechanism whereby the plant responds naturally to water deficit. Tomatoes have considerable physiological plasticity under abiotic stress, partly through the action of stress-responsive genes, such as the calmodulin-like genes that improve drought tolerance (Munir et al., 2016). Furthermore, genetic strategies that enhance stress tolerance in tomatoes could lead to an increase in the accumulation of ascorbic acid, a key antioxidant and fruit quality marker (Li et al., 2019). While these genetic insights are valuable, physiological indicators, such as spectral indices, provide a more practical, non-destructive method for real-time water stress detection. Building on this, there is a clear need to link these physiological measurements to precise irrigation strategies to optimize yield and quality. Therefore, the current

study investigated the effects of different water contents on changes in plant physiology and evaluated the optimal water content for producing cherry tomatoes in a greenhouse under tropical conditions.

## Materials and Methods

### Tomato planting and experimental design

The experiment was conducted in a greenhouse, at Kasetsart University, Bangkok, Thailand (13°51'13.5"N, 100°34'09.2"E) during October 2021–January 2022. Seeds of the cherry tomato 'Sweet Boy' (a yellow-orange tomato, which is a hybrid of Chia Tai) were planted in 104-cell seedling trays, using peat moss as the planting material. The seedlings were transplanted into 20 cm diameter × 15 cm height (approximately 5 L) white-colored planting pots using a mixture of chopped coconut husks-to-coconut coir at a ratio of 1:1 by volume. Each pot was placed on a saucer and arranged within a lined plot. The nutrient solution was Resh Tropical dry summer (Resh, 2012) that was applied to the seedlings at 1 wk after transplanting. Throughout the experiment, the electrical conductivity and pH were controlled in the ranges 2.4–3.4 mS/cm and 5.5–6.0, respectively. The experiment was arranged in a completely randomized design with four water treatment levels based on pot water capacity (PC): 60%PC, 80%PC, 100%PC (the control) and 120%PC), with five replications per treatment and one plant per replication. The water content in the growing medium was provided by saturating the growing medium in the pot and then the water was allowed to drain for 24 hr and 100%PC was calculated from the difference between the weight of the growing medium after drainage and the initial dry weight of the growing medium. The PC water level was controlled using the potted plant weighing method (Pereira and Kozłowski, 1976). The water supply for 100%PC was 0.12 L/pot/d, 0.74 L/pot/d and 1.08 L/pot/d at the vegetative, flowering, and fruit set stages, respectively

(Table 1). Light intensity, temperature and relative humidity in the greenhouse were recorded every 30 min throughout the experiment. In addition, temperature and relative humidity were used to calculate the vapor pressure deficit (VPD) according to Noh and Lee (2022).

**Table 1** Amount of water applied per tomato plant per day in each growth stage for different pot water capacity treatments

Pot water capacity (%)	Water content in each growth stage (L/pot/day)			
	Seedling	Vegetative	Flowering	Fruit set
60	0.02	0.02	0.24	0.51
80	0.02	0.03	0.46	0.80
100	0.02	0.12	0.74	1.08
120	0.02	0.38	1.05	1.39

### Measurement of physiological changes

Physiological changes (leaf reflectance, spectral indices, leaf greenness index, gas exchange parameters and quantum yield efficiency parameters) were estimated three times according to the growth stage of cherry tomato: the vegetative stage (6 wk after transplanting, WAT), the flowering stage (50% flowering, 9 WAT) and the fruit setting stage (after the first fruit harvest, 16 WAT). Different physiological changes were measured in the leaf at the 3<sup>rd</sup> position from the highest leaf at the time.

Leaf reflectance was obtained using a spectroradiometer (PolyPen RP410 UVIS; Photon Systems Instruments; Czech Republic) in the wavelength range 380–790 nm. Later, spectral indices consisting of the normalized difference vegetation index (NDVI), the normalized difference red-edge index (NDRE) and the photochemical reflectance index (PRI) were calculated using the formulas shown in Table 2. All data was collected during 0900–1200 hours.

Leaf greenness index was measured between 0900 and 1200 h using a chlorophyll meter (SPAD-502; Minolta; Japan). The greenness index was recorded three times in three leaflets, with the mean ± SD used to represent the greenness index of that leaf.

**Table 2** Information on spectral indices used.

Acronym	Spectral index	Formula	Reference
NDVI	Normalized difference vegetation index	$NDVI = (NIR - Red) / (NIR + Red)$	Rouse et al. (1973)
NDRE	Normalized difference red-edge index	$NDRE = (R_{790} - R_{720}) / (R_{790} + R_{720})$	Barnes et al. (2000)
PRI	Photochemical reflectance index	$PRI = (R_{570} - R_{531}) / (R_{570} + R_{531})$	Gamon et al. (1992)

NIR = near-infrared reflectance (898–913 nm); Red = red reflectance (668–683 nm);  $R_{xxx}$  = reflectance at xxx nm (Reynolds et al., 2012).

Gas exchange parameters were measured using a portable photosynthesis system (LI-6400XT; LI-COR Environmental; USA) with an air flow rate of 500  $\mu\text{mol/s}$ , a light intensity of 800  $\mu\text{mol/m}^2/\text{s}$  and a  $\text{CO}_2$  concentration of 400 parts per million. The net photosynthetic rate, stomatal conductance and transpiration rate (E) were obtained during 0800–1100 hours. Then, the water use efficiency (WUE) was calculated from the ratio of the net photosynthetic rate to the transpiration rate.

Quantum yield efficiency parameters were measured using a pulse amplitude modulation fluorometer (MINI-PAM-II; Walz; Germany) during 0900–1200 hours. The minimal and maximal fluorescence yields of the dark-adapted state ( $F_m$ ) in the leaves were assessed after 30 min of dark adaptation. After that, leaves were illuminated with actinic light (800  $\mu\text{mol/m}^2/\text{s}$ ) for 15 s. The methods of Maxwell and Johnson (2000) were used to calculate all the quantum yield efficiency parameters, consisting of the maximum quantum yield of photosystem II (PSII) photochemistry ( $F_v/F_m$ ), the effective quantum yield of PSII photochemistry ( $Y(II)$ ), the photochemical quenching coefficient (qP) and nonphotochemical quenching (NPQ).

#### *Analysis of cherry tomato fruit quantity and quality*

The cherry tomatoes began to produce fruit approximately 16 wk after transplanting. The fruits at a yellow-orange color stage were harvested every 3–4 d until the end of production. The fruit quantity was evaluated based on the fruit weight per fruit, width and length. In addition, all fruits in a plant were measured to determine the total yield per plant.

After harvest, 2–5 tomato fruits per replication were selected randomly to analyze fruit firmness, the total soluble solids (TSS), the titratable acidity (TA) and the ascorbic acid, lycopene and  $\beta$ -carotene contents. Each tomato fruit was analyzed twice: at first harvesting and then approximately 1 wk after the first harvest. The firmness of each tomato was measured using a penetrometer (Effegi; Italy) and the TSS was analyzed using a hand refractometer (PR-101 alpha; Atago; Thailand). The TA was analyzed based on 1 mL of tomato juice homogenized in 50 mL of distilled water. Then, the TA was obtained by titrating with 0.1 N NaOH and a calculation referring to the percentage of citric acid (AOAC International, 2000). The ascorbic acid contents were analyzed using an RQ-flex reflectometer (Merck; Germany) according to Takebe and Yoneyama (1995). The lycopene and  $\beta$ -carotene contents in the tomato pulp samples were extracted in a mixed solution of hexane-to-acetone-to-ethanol ratio of 2:1:1. Then, the lycopene and  $\beta$ -carotene contents were analyzed according to Anthon and Barrett (2007).

#### *Statistical analysis*

The data were analyzed using one-way analysis of variance (ANOVA), and mean differences were compared using Tukey's honestly significant difference (HSD) test at the 95% confidence level. Pearson's correlation coefficient was utilized to determine correlations among parameters and a heatmap was generated based on the coefficient of determination. All statistical analyses were carried out using the IBM SPSS Statistics for Windows software (version 22.0; IBM Corp.; Armonk, NY, USA). Data are presented as mean  $\pm$  SD.

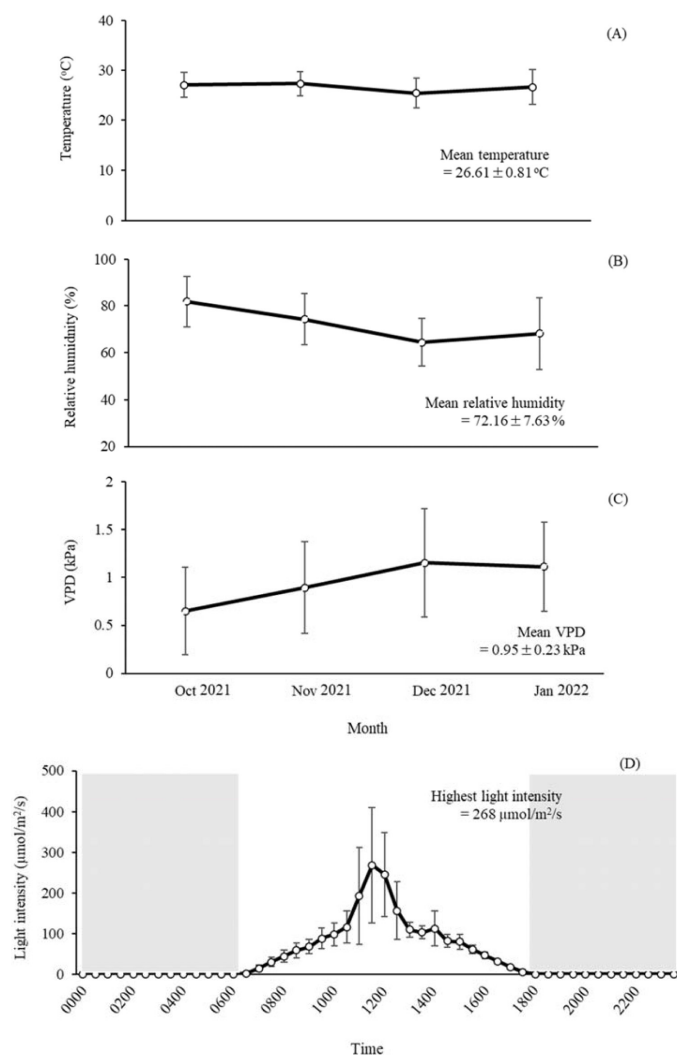
## **Results and Discussion**

### *Greenhouse weather and water content in growing medium during tomato planting*

Values for daily temperature, relative humidity and VPD during cultivation in the greenhouse were in the ranges  $25.4 \pm 3.0$ – $27.3 \pm 2.4^\circ\text{C}$ ,  $64.4 \pm 10.2$ – $81.9 \pm 10.9\%$  and  $0.65 \pm 0.45$ – $1.12 \pm 0.56$  kPa, respectively (Figs. 1A–1C). The mean highest light intensity in the greenhouse was  $268 \pm 142$   $\mu\text{mol/m}^2/\text{s}$  (Fig. 1D). In addition, the water supplied in each treatment (60%PC, 80%PC, 100%PC and 120%PC) in the different growth stages is shown in Tables 1 and 3. Based on these results, during fruit set, the tomatoes required a higher water content than during the flowering and vegetative stages (Tables 1 and 3). This was consistent with Lui et al. (2019), who reported that tomato plants reaching water deficiency during the vegetative growth stage had a greater yield than in the fruit set and fruit development stages. In the current experiment, watering was applied at 100%PC (the control), 60%PC and 80%PC, which were equivalent to only 0.40 and 0.66 times the control, respectively. In contrast, the total amount of water applied throughout the entire tomato production cycle at 120%PC was 1.48 times greater than that of the control treatment (Table 3).

**Table 3** Amount of water applied to tomato plants in each growth stage for different pot water capacity treatments.

Pot water capacity (%)	Water content in each growth stage (L/plant)				Total water (L/plant)
	Seedling	Vegetative	Flowering	Fruit set	
60	0.45	0.50	4.01	8.73	13.69
80	0.45	0.71	7.77	13.56	22.49
100	0.45	2.69	12.64	18.43	34.21
120	0.45	8.67	17.82	23.60	50.53

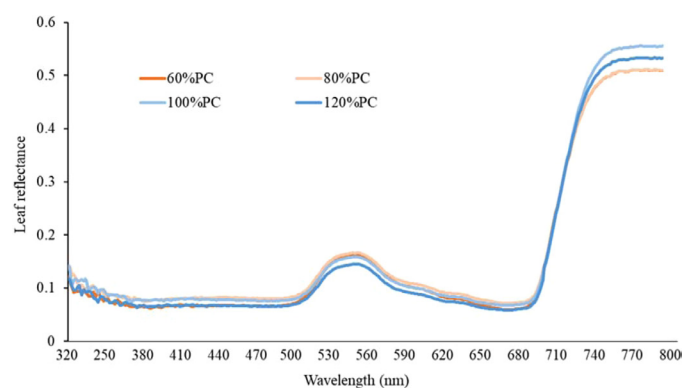


**Fig. 1** Internal greenhouse changes from October 2021 to January 2022 for: (A) temperature; (B) relative humidity; (C) vapor pressure deficit (VPD); and (D) mean daily light intensity. Data are presented as mean  $\pm$  SD and gray shaded area indicates periods of darkness.

### Changes in leaf reflectance with different pot capacities

The spectral reflectance properties from 380–790 nm of the tomato leaves grown using the various PC conditions were measured using the spectrometer during the vegetative stage, with wavelengths recorded in the range 400–700 nm (visible light) indicating low leaf reflectance whereas wavelengths above 700 nm (near-infrared (NIR) light) indicated high leaf reflectance (Fig. 2). Among the various PC levels tested, the significantly ( $p < 0.01$ ) lowest leaf reflectance was from the treatment with 120%PC in the wavelength range 510–680 nm. On the other hand, the leaf reflectance wavelengths from the 60%PC and 80%PC treatments had the significantly ( $p < 0.01$ )

lowest values of 740–790 nm (Fig. 2). Spectral reflectance provides useful data for plant stress detection, since the readings provide near real-time and non-destructive estimation of plant stress (Katsoulas et al., 2016). Leaf reflectance can be applied for monitoring water stress in many plants. Reflectance in the wavelength range of 750–800 nm is mostly related to leaf water status because the leaf reflectance of water-stressed plants will increase in the NIR region due to radiation scattering resulting from the increased air space in the sponge cavities of mesophyll cells (Katsoulas et al., 2016). When plants were close to wilting from water stress, increased NIR reflectance was observed (Peñuelas et al. 1993).

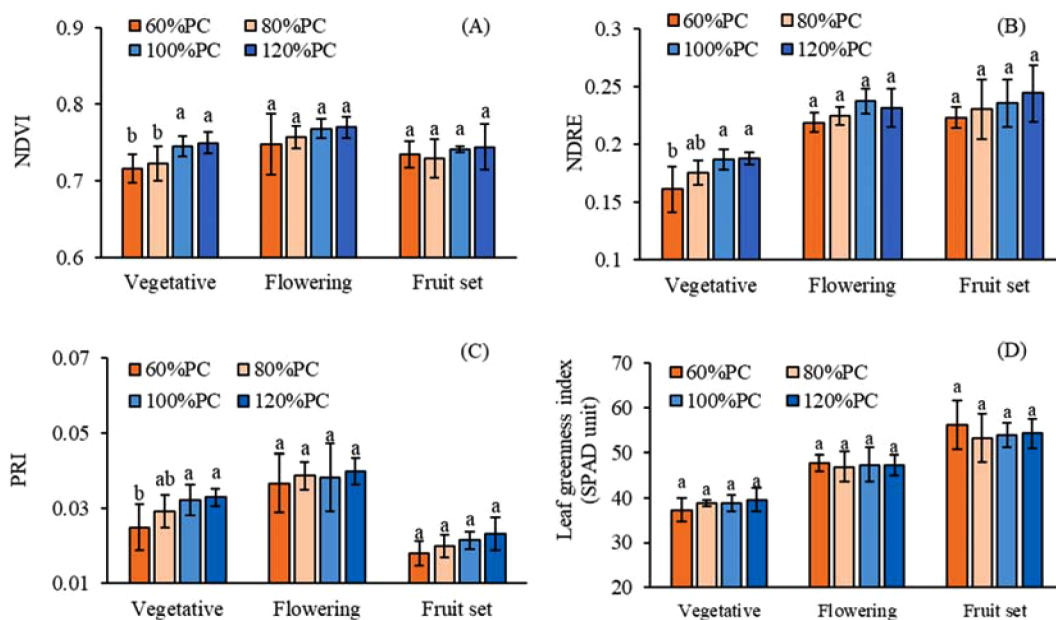


**Fig. 2** Leaf reflectance spectra of tomato plants under different levels of pot water capacity (PC). Reflectance was measured across the 320 – 800 nm wavelength range. Each curve represents the mean  $\pm$  SD.

### Effect of pot water capacity on spectral indices and leaf greenness index

The spectral indices (NDVI, NDRE and PRI) were calculated from various reflectance values, as shown in Table 2. Based on these results, 60%PC and 80%PC significantly ( $p < 0.05$ ) reduced NDVI during the vegetative stage (Fig. 3A). The available water content at 60%PC produced the lowest NDRE and PRI values during the vegetative stage (Figs. 3B and 3C). However, the different PC levels did not alter the NDVI, NDRE and PRI values for tomato leaves during the flowering and fruit setting stages (Figs. 3A–3C). Among the different plant stages, the leaf greenness index tended to increase from the vegetative stage to the fruit setting stage; however, leaf greenness indices did not significantly ( $p < 0.05$ ) differ among the water treatments within each growth stage (Fig. 3D). More than 150 spectral indices have been reported; however, only some spectral indices were indicative of water stress (Katsoulas et al., 2016).





**Fig. 3** Effect of different levels of pot water capacity (PC) at each growth stage of tomato 'Sweet Boy' on: (A) normalized difference vegetation index (NDVI); (B) normalized difference red edge index (NDRE); (C) photochemical reflectance index (PRI); (D) leaf greenness index. Bars and error bars represent the mean and SD ( $n = 5$ ). Different lowercase letters above bars within the same growth stage indicate significant differences ( $p < 0.05$ ).

Spectral indices can be classified based on their function in the plant, for example leaf structure-related indices, such as the NDVI, compared to NDRE and xanthophyll cycle-related indices, such as PRI (Ihuoma and Madramootoo, 2019a; Ihuoma and Madramootoo, 2019b). The NDVI, NDRE and PRI are commonly used to analyze water stress in a plant (Gamon et al., 1992; Katsoulas et al., 2016). In the current study, high NDVI, NDRE and PRI values were recorded in the tomato plants grown with 100%PC and 120%PC, indicating that watering at these levels was sufficient for the tomatoes. These findings aligned with the decrease in NDVI and PRI reported in tomatoes subjected to water stress (Ihuoma and Madramootoo, 2019b). The lack of irrigation disrupted the mesophyll cell structure, leading to a reduction in NIR reflectance (Stamford et al., 2023), which contributed to the decline in NDVI under drought conditions. The decrease in PRI caused by drought stress indicated that plants were unable to dissipate excess heat through the xanthophyll cycle under stressed conditions (Ihuoma and Madramootoo, 2019b). In addition, NDRE was identified as the most effective spectral index for estimating leaf water status in grapevines (Tang et al., 2022). On the other hand, the different available water contents did not affect the leaf greenness index of the tomato leaves, perhaps because greenhouse-grown tomatoes have a decreased chlorophyll content which could be reflected in the leaf greenness index when subjected to moderate (45–50% of field capacity) or severe water stress (35–40% of field capacity),

according to Yuan et al. (2016). This finding was consistent another study where photosynthetic pigments were affected only by severe or combined stress (Rodrigues et al., 2024). Therefore, the stress treatments in the current study were limited to mild-to-nearly moderate water stress. Thus, PRI and NDRE proved to be sensitive tools for early water stress detection in tomato, successfully differentiating among non-water stress (100%PC and 120%PC), mild (80%PC) and nearly moderate (60%PC) stress levels, whereas direct chlorophyll measurements, such as the leaf greenness index, showed no effect.

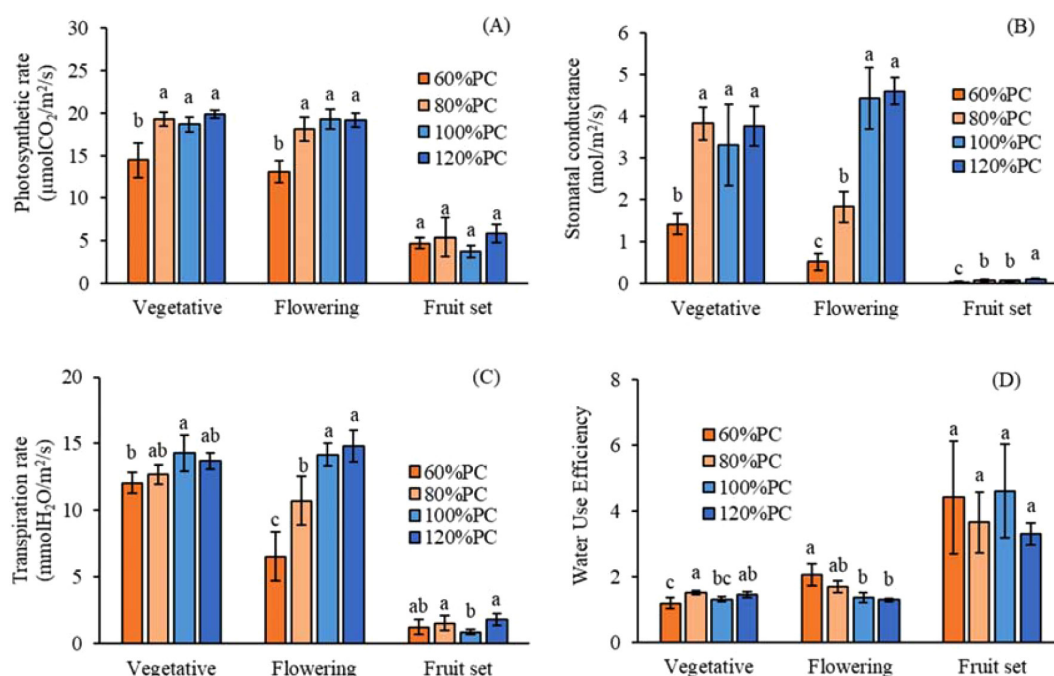
#### *Effect of pot water capacity on gas exchange*

Leaf gas exchange was determined to indicate the water stress in the tomatoes. Analysis of the results revealed that watering with only 60%PC significantly ( $p < 0.01$ ) reduced the photosynthetic rate during the vegetative and flowering stages, whereas the photosynthetic rates for 80–120%PC were not significantly different (Fig. 4A), indicating that the water content at 60%PC was insufficient for tomato plant requirements. A decrease in photosynthesis is one of the responses by a plant to water stress (Osakabe et al., 2014). However, the photosynthetic rates in all the current treatments during the fruit setting stage were greatly reduced compared to the vegetative and flowering stages (Fig. 4A). This might have been due to a source-sink imbalance in the tomato plants after fruit set, as the developing

fruits became dominant sinks (Fischer et al., 2012). Changes in the photosynthetic rate were associated with changes in stomatal conductance. Tomato plants receiving available water content at 60%PC had significantly ( $p < 0.01$ ) decreased stomatal conductance in both the vegetative and flowering stages (Fig. 4B). The stomatal conductance is indicative of stomatal opening, since when stomata close, the stomatal conductance drops (Farquhar and Sharkey, 1982), leading to reduced  $\text{CO}_2$  diffusion through the stomata, causing a decrease in photosynthesis (Osakabe et al., 2014). This could have been the reason for the lowest photosynthetic rate in the 60%PC treatment.

Watering at 60%PC and 80%PC during the vegetative stage tended to significantly ( $p < 0.01$ ) decrease the transpiration rate compared to watering at the control level of 100%PC (Fig. 4C). Furthermore, tomatoes grown with 60%PC and 80%PC had significantly lower transpiration rates than those watered with 100%PC and 120%PC (Fig. 4C). A decrease in the transpiration rate is one water stress defense mechanism (Ritchie, 1998). During the fruit setting stage, the transpiration rate in all treatments was lowest compared to the other growth stages (Fig. 4C), which was related to the decrease in stomatal conductance. Calculating the WUE based on the ratio of the photosynthetic rate to the transpiration rate showed that an available water content of 60%PC had the lowest WUE value among the treatments during the vegetative stage (Fig. 4D). However, during the flowering stage, the treatment with

60%PC had the highest WUE (Fig. 4D), perhaps because the tomato plants could adjust to growing under water stress by closing stomata and decreasing the transpiration rate, resulting in a high WUE. In addition, WUE is influenced by VPD, which tended to increase from November onwards, coinciding with the flowering stage of tomato plants (Fig. 1C). However, under drought conditions, the negative correlation between WUE and VPD was less pronounced because soil water deficit is the primary driver of stomatal closure, making the plant's reaction to dry air much weaker (Wang et al., 2024). The decrease in the transpiration rate due to stomatal closure is one process recognized to maintain a high level of WUE (Hatfield and Dold, 2019). During the fruit setting stage, all treatments had the same level of WUE (Fig. 4D). Throughout the entire tomato production cycle, watering at 100%PC produced the same WUE as watering at 120%PC (Fig. 4D) because watering at 100%PC and 120%PC produced the same rates of photosynthesis and transpiration (Figs. 4A and 4C). During November–January, the VPD in the greenhouse was in the range 0.9–1.1 kPa (Fig. 1C), which was within the optimal range (0.9–2.2 kPa) for tomato production in the greenhouse (Yu et al., 2024). When the ambient VPD is not too high, the evaporation rate of water from the growing medium is not high (Grossiord et al., 2020). Therefore, watering to 100%PC and 120%PC was likely to result in the same moisture content in the growing media, with both reaching near saturation at approximately 100%.



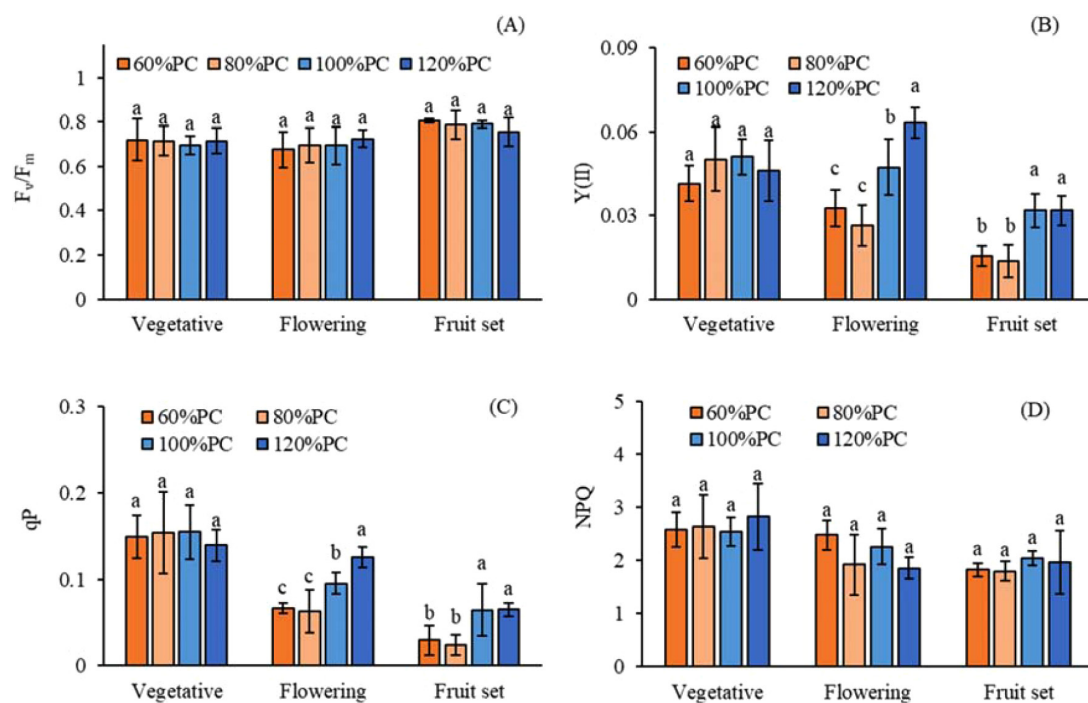
**Fig. 4** Effect of different levels of pot water capacities (PC) at each growth stage of tomato 'Sweet Boy' on: (A) net photosynthetic rate; (B) stomatal conductance; (C) transpiration rate; (D) water use efficiency. Bars and error bars represent the mean and SD ( $n = 5$ ). Different lowercase letters above bars within the same growth stage indicate significant differences ( $p < 0.05$ ).

### Changes in quantum yield efficiency with different pot capacities

The photosynthesis efficiency was based on the quantum yield efficiency. Based on the results, the maximum quantum yields of PSII photochemistry ( $F_v/F_m$ ) of tomato leaves in all the growth stages of every treatment were not significantly different (Fig. 5A). The non-significant difference in  $F_v/F_m$  was related to the changes PRI (Figs. 3C and 5A). The decrease in PRI strongly correlated with  $F_v/F_m$  and its related parameters in PSII efficiency (Gamon et al., 1997), which would explain why both PRI and  $F_v/F_m$  had similar responses to water stress in the current study. The  $F_v/F_m$  values were in the ranges 0.70–0.72, 0.68–0.73 and 0.75–0.81 for the vegetative, flowering and fruit setting stages, respectively (Fig. 5A). The  $F_v/F_m$  value could be used as a physiological stress indicator as, generally, healthy plants have an  $F_v/F_m$  value in the range 0.79–0.83. If the  $F_v/F_m$  value is lower than 0.79, the plant is subjected to some environmental stress and chlorophyll fluorescence will appear, leading to photoinhibition (Björkman and Demmig, 1987; Maxwell and Johnson, 2000). In the current study, the mean temperature was still appropriate for tomato production (Sato et al., 2000). Therefore, the chlorophyll fluorescence that occurred in some treatments and in some

growth stages in the current study might have been caused by the genetics of this tomato cultivar.

Other quantum yield efficiency parameters under different pot capacities were also estimated. Based on those results, the water content at 60%PC and 80%PC significantly ( $p < 0.01$ ) decreased Y(II), along with qP during the flowering and fruit setting stages compared to the control (100%PC), as shown in Figs. 5B and 5C. Furthermore, tomatoes in the 100%PC treatment had Y(II) and qP values as high as those for the 120%PC treatment during the fruit setting stage (Figs. 5B and 5C). Y(II) refers to the quantum yield efficiency of PSII under light conditions, whereas qP indicates the ratio of the opened-to-closed reaction centers of PSII (Maxwell and Johnson, 2000). An increase in Y(II) indicates that the plant is not susceptible to photoinhibition (Hichem et al., 2009), while a high qP indicates separation of the electron charge in the reaction center, leading to a large amount of ATP production that can be used in photosynthesis (Guo et al., 2006). In addition to qP, nonphotochemical quenching (NPQ) was examined. The different pot water capacities did not alter NPQ in any of the growth stages (Fig. 5D). Notably, a decrease in qP is not necessarily associated with an increase in NPQ (Calatayud and Barreno, 2004).



**Fig. 5** Effect of different levels of pot water capacities (PC) at each growth stage of tomato 'Sweet Boy' on: (A) maximum quantum yield of PSII photochemistry ( $F_v/F_m$ ); (B) effective quantum yield of PSII photochemistry (Y(II)); (C) photochemical quenching coefficient (qP); and (D) nonphotochemical quenching (NPQ). Bars and error bars represent mean and SD ( $n = 5$ ). Different lowercase letters above bars within the same growth stage indicate significant differences ( $p < 0.05$ ).



### Quantity and quality of cherry tomatoes

The yield was based on the direct harvest of the fruit on the plants at the yellow-orange color stage. The fruit weight, total marketable yield and fruit size data are summarized in Table 4. The fruit weight was higher for the tomatoes grown using a greater pot water capacity; however, there were no significant ( $p \geq 0.05$ ) differences in fruit length among the treatments. Compared to the fully watered treatments, fruit weight was significantly ( $p < 0.01$ ) reduced in the 60%PC treatment and tended to be lower at 80%PC ( $p < 0.05$ ). However, fruit weights among the 80%PC, 100%PC and 120%PC treatments were not significantly different (Table 4). In addition, the fruit weights from the treatments using 80%–120%PC were not significantly different; however, watering to only 60%PC and 80%PC significantly reduced and tended to reduce the tomato fruit weight, respectively (Table 4). In addition, the total marketable yield exhibited the same trend of fruit weight. Based on these results, watering at only 60%PC and 80%PC significantly reduced the total marketable yield by 3.54 and 2.01 times, respectively, compared to the control (100%PC), as shown in Table 4. These data were consistent with the results from another study where there was a decrease in fruit weight when a 50% water reduction was applied (Pernice et al., 2010). Altogether, these results indicated that 100%PC was sufficient for cherry tomatoes to produce fruit and that excessive watering was unnecessary to grow cherry tomatoes in a greenhouse. Without any water restriction, metabolic activity was maintained in the vegetable at adequate levels, capturing CO<sub>2</sub> from the atmosphere and utilizing nutrients in the substrate and allowing better productive responses by the adequate production of photo-assimilates (Melo et al., 2010). The largest diameter of fruits was obtained at 120%PC, with a decreasing trend with a reduction in the water content.

**Table 4** Fruit weight, diameter and length of cherry tomato ‘Sweet Boy’ grown with different levels of pot water capacity

Pot water capacity (%)	Fruit weight (g)	Fruit diameter (cm)	Fruit length (cm)	Total marketable yield (g/plant)
60	2.55±0.94 <sup>b</sup>	1.68±0.20 <sup>b</sup>	2.13±0.49	27.48±9.61 <sup>b</sup>
80	3.67±1.20 <sup>ab</sup>	1.69±0.16 <sup>b</sup>	2.30±0.26	46.91±13.18 <sup>b</sup>
100	4.80±0.51 <sup>a</sup>	1.65±0.21 <sup>b</sup>	2.29±0.12	97.36±31.44 <sup>a</sup>
120	5.27±0.75 <sup>a</sup>	1.91±0.13 <sup>a</sup>	2.44±0.56	114.91±13.86 <sup>a</sup>

Mean ± SD ( $n = 5$ ) within each column followed by different lowercase superscript letters are significantly different ( $p < 0.05$ ). Absence of superscript denote non-significant differences ( $p \geq 0.05$ ).

Fruit weight followed the same trend as total marketable yield. Irrigation at 100%PC and 120%PC resulted in higher yields compared to 60%PC and 80%PC (Table 4), indicating that water stress reduced both fruit number and fruit size. The reduction in fruit diameter could have been a result of a reduction in the rate of cell division and elongation due to a water deficit (Taiz and Zeiger, 2010).

In addition to the quantity of tomato fruit from the different pot capacities, fruit quality parameters were measured, consisting of fruit firmness, TSS, TA and the TSS-to-TA ratio. The results showed that there was no significant ( $p \geq 0.05$ ) difference in fruit firmness among the treatments (Table 5). The value of TSS increased with decreased pot water capacity. However, the TSS values for the 60%–100%PC treatments were not significantly different, whereas the TSS value in tomato fruit from 120%PC was significantly ( $p < 0.05$ ) lower than for 60%PC (Table 5). Based on these results, maintaining the water content at 60%–100%PC was adequate for the control of tomato fruit quality. Furthermore, a decrease in the amount of applied water to 60% field capacity was reported to have significantly improved fruit quality parameters (Chand et al., 2021). In the current study, the TA was significantly ( $p < 0.01$ ) different among the pot capacities, varying from 0.53% at 60%PC to 1.05% at 120%PC. This variation might have been due to variability in the fruit weight because the large-sized tomato fruit usually had higher acidity (Tigist et al., 2013). The ratio of TSS-to-TA in each treatment was estimated, with the analysis indicating that the water supply at 60%–100%PC tended to increase the TSS-to-TA ratio (Table 5). This ratio is regarded as an important parameter indicating the flavor quality of tomatoes (Xu et al., 2018). Thus, the high TSS-to-TA ratio in the 60%–100%PC treatments indicated that those cherry tomatoes were tastier than tomatoes grown with 120%PC.

**Table 5** Fruit firmness, total soluble solids (TSS), titratable acidity (TA) and TSS-to-TA ratio of cherry tomato ‘Sweet Boy’ grown with different levels of pot water capacity

Pot water capacity (%)	Fruit firmness (N/cm <sup>2</sup> )	TSS (°Brix)	TA (%)	TSS-to-TA ratio
60	15.55±3.52	9.48±1.03 <sup>a</sup>	0.53±0.09 <sup>c</sup>	18.17±3.96 <sup>a</sup>
80	15.67±3.88	8.51±2.07 <sup>ab</sup>	0.77±0.08 <sup>b</sup>	10.97±2.03 <sup>b</sup>
100	15.60±4.54	8.04±1.58 <sup>ab</sup>	0.79±0.12 <sup>b</sup>	10.26±2.19 <sup>b</sup>
120	12.22±3.09	6.98±0.71 <sup>b</sup>	1.05±0.13 <sup>a</sup>	6.66±0.43 <sup>b</sup>

Mean ± SD ( $n = 5$ ) within each column followed by different lowercase superscript letters are significantly different ( $p < 0.05$ ). Absence of superscript denote non-significant differences ( $p \geq 0.05$ ).

The cherry tomatoes grown with different pot capacities were analyzed for their phytonutrients, consisting of the ascorbic acid, lycopene and  $\beta$ -carotene contents. The analysis of these results revealed that the ascorbic acid content of the tomato fruit improved with a reduction in the pot water capacity (Table 6), although there was no significant difference between the 60%PC and 80%PC treatments (Table 6). These results were consistent with Chand et al. (2021), who reported that a deficit in irrigation increased the ascorbic acid content in tomato fruits. In addition, it is assumed that a higher TSS content in fruits (due to the lower water supply) promotes ascorbic acid synthesis (Dumas et al., 2003). The increase in ascorbic acid, which acts as an antioxidant during water stress, might have resulted from the oxidative stress defensive mechanism in plants (Jiang et al., 2002). In tomatoes, drought stress induced oxidative stress, which was mitigated by increased ascorbic acid levels due to its strong antioxidant activity (Munir et al., 2016; Li et al., 2019). At the molecular level, this response is tightly regulated; for example, the increased ascorbic acid accumulation observed in the current study was consistent with the known induction of key synthesis pathway genes, such as the Myo-inositol oxygenase family, by drought stress (Munir et al., 2020).

In the current study, the lycopene contents were in the range 1.68–4.81 mg/kg fresh weight. The water contents at 60%PC and 80%PC resulted in significantly ( $p < 0.05$ ) higher lycopene contents in the tomato fruits than at 100%PC and 120%PC (Table 6). It seemed that a decrease in the water content resulted in a considerable increase in the lycopene content, which was consistent with Coyago-Cruz et al. (2022), who reported that the application of a regulated deficit in irrigation increased the lycopene content in tomato fruits. Generally, there is genetic control of the accumulation of secondary metabolites, such as lycopene, under drought conditions (Li et al., 2019; Munir et al., 2020). The ability of cultivars to enhance fruit quality is determined by natural variation in key regulators, such as the transcription factor *GAME9* (Yu et al., 2020). However, in the current study, there were no significant differences in the  $\beta$ -carotene contents in the tomatoes from any of the treatments (Table 6).

**Table 6** Ascorbic acid, lycopene and  $\beta$ -carotene contents of cherry tomato ‘Sweet Boy’ grown with different pot capacities

Pot water capacity (%)	Ascorbic acid (mg/kg FW)	Lycopene (mg/kg FW)	$\beta$ -Carotene (mg/kg FW)
60	9.11 $\pm$ 2.34 <sup>ab</sup>	4.24 $\pm$ 1.98 <sup>a</sup>	4.03 $\pm$ 1.40
80	10.42 $\pm$ 0.73 <sup>ab</sup>	4.77 $\pm$ 2.09 <sup>a</sup>	4.62 $\pm$ 1.71
100	7.38 $\pm$ 2.43 <sup>b</sup>	1.70 $\pm$ 0.92 <sup>b</sup>	4.77 $\pm$ 2.40
120	4.70 $\pm$ 1.52 <sup>c</sup>	1.68 $\pm$ 1.01 <sup>b</sup>	3.44 $\pm$ 1.17

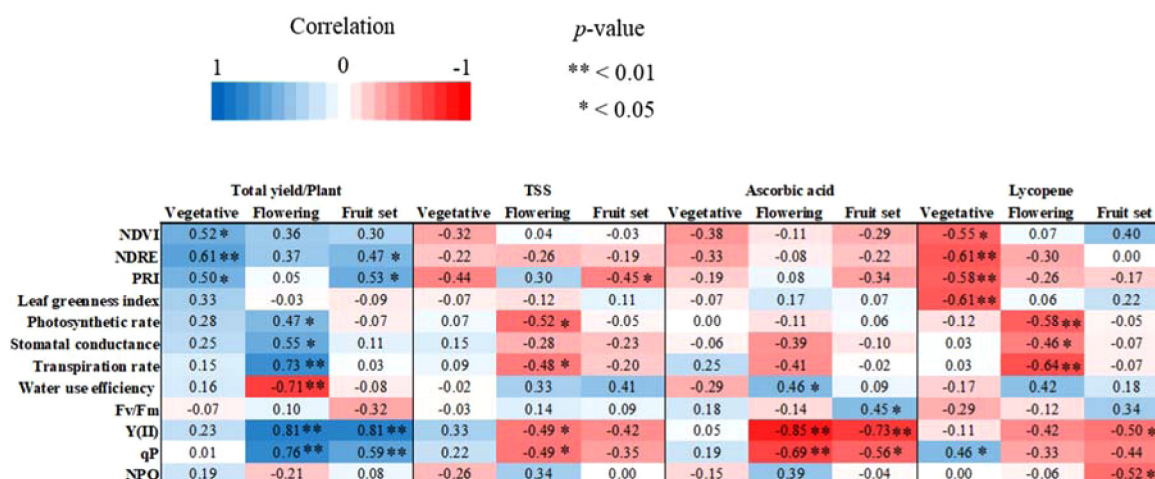
FW = fresh weight.

Mean  $\pm$  SD (n = 5) within each column followed by different lowercase superscript letters are significantly different ( $p < 0.05$ ). Absence of superscript denote non-significant differences ( $p \geq 0.05$ ).

Although irrigation at 60%PC resulted in higher TSS levels (Table 5) and in the ascorbic acid and lycopene contents (Table 6), these quality improvements came at the expense of reduced fruit yield (Table 4). In cherry tomatoes, fruit size, sweetness and juiciness are key attributes that influence consumer preference (Casals et al., 2018). The findings of the current study confirmed that irrigation at 100%PC provided the optimal balance between maximum yield and acceptable fruit quality.

### Correlation between physiological responses and yields

The current study examined the correlations between yield, fruit quality and physiological responses to better understand how production and quality traits are influenced by plant physiological status. Based on this analysis, changes in the NDRE at the vegetative stage were positively correlated with total yield but negatively correlated with lycopene content (Fig. 6). NDRE has been used widely to assess drought stress in plants (Gamon et al., 1992; Katsoulas et al., 2016), which was consistent with the current findings, where irrigation at 100%PC and 120%PC resulted in higher NDRE values during the vegetative stage (Fig. 3A). In addition, low photosynthetic and transpiration rates during the flowering stage were significantly associated with increases in the TSS ( $p < 0.05$ ) and the lycopene content ( $p < 0.01$ ), as indicated by their negative correlations (Fig. 6). Notably, irrigation at 100%PC had the highest photosynthetic rate during the flowering stage and produced an acceptable TSS level ( $>5^\circ\text{Brix}$ ), which is suitable for good-tasting table tomatoes (Padmanabhan et al., 2016). However, it did not achieve the standard lycopene content required in yellow cherry tomatoes (Chang et al., 2024). Furthermore, Y(II) and qP during the flowering and fruit set stages were positively correlated with total yield and negatively correlated with ascorbic acid content (Fig. 6). Although insufficient irrigation reduced tomato yield (Colimba-Limaico et al., 2022), elevated levels of ascorbic acid have been linked to increased oxidative stress responses (Munir et al., 2016; Li et al., 2019). Therefore, reductions in Y(II) and qP during the flowering and fruit set stages might serve as potential diagnostic tools for water stress detection in cherry tomatoes. Notably, the findings from the current study were based on a specific cherry tomato cultivar under controlled pot-based conditions. Therefore, future studies should be undertaken on different cultivars and on a larger commercial greenhouse scale to confirm the broader applicability of these diagnostic tools.



**Fig. 6** Heatmap of Pearson's correlation coefficients illustrating relationships between physiological responses and cherry tomato yield parameters, where red and blue color gradients indicate positive and negative correlations, respectively, NDVI = normalized difference vegetation index, NDRE = normalized difference red-edge index, PRI = photochemical reflectance index,  $F_v/F_m$  = maximum quantum yield of PSII photochemistry,  $Y(II)$  = effective quantum yield of PSII photochemistry, qP = photochemical quenching coefficient, NPQ = nonphotochemical quenching, TSS = total soluble solids

## Conflict of Interest

The authors declare that there are no conflicts of interest.

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## References

- Anthon, G., Barrett, D.M. 2007. Standardization of a rapid spectrophotometric method for lycopene analysis. *Acta Horti*. 758: 111–128. doi.org/10.17660/ActaHortic.2007.758.12
- AOAC International. 2000. Acidity (titratable) of fruit products. AOAC Official Method 942.15. Official Methods of Analysis of AOAC International. AOAC International, Gaithersburg, MD, USA.
- Beckles, D.M. 2012. Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biology and Technology* 63: 129–140. doi.org/10.1016/j.postharvbio.2011.05.016
- Björkman, O., Demmig, B. 1987. Photon yield of  $O_2$  evolution and chlorophyll fluorescence characteristics at 77K among vascular plant of diverse origins. *Planta* 170: 489–504. doi: 10.1007/BF00402983.
- Calatayud, A., Barreno, E. 2004. Response to ozone in two lettuce varieties on chlorophyll a fluorescence, photosynthetic pigments and lipid peroxidation. *Plant Physiol. Bioch.* 42: 549–555. doi: 10.1016/j.plaphy.2004.05.002.
- Cantero-Navarro, E., Romero-Aranda, R., Fernández-Muñoz, R., Martínez-Andújar, C., Pérez-Alfocea, F., Albacete, A. 2016. Improving agronomic water use efficiency in tomato by rootstock-mediated hormonal regulation of leaf biomass. *Plant Sci.* 251: 90–100. doi.org/10.1016/j.plantsci.2016.03.001
- Casals, J., Rivera, A., Sabaté, J., del Castillo, R.R., Simó, J. 2019. Cherry and fresh market tomatoes: differences in chemical, morphological, and sensory traits and their implications for consumer acceptance. *Agronomy* 9: 9. doi: 10.3390/agronomy9010009
- Chand, J.B., Hewa, G., Hassanli, A., Myers, B. 2021. Plant biomass and fruit quality response of greenhouse tomato under varying irrigation level and water quality. *Aust. J. Crop Sci.* 15: 716–724. doi: 10.21475/ajcs.21.15.05.p3052
- Chang, Y., Zhang, X., Wang, C., Ma, N., Xie, J., Zhang, J. 2024. Fruit quality analysis and flavor comprehensive evaluation of cherry tomatoes of different colors. *Foods* 13: 1898. doi.org/10.3390/foods13121898
- Clinton, S.K. 1998. Lycopene: chemistry, biology, and implications for human health and disease. *Nutr. Rev.* 56: 35–51. doi.org/10.1111/j.1753-4887.1998.tb01691.x
- Colimba-Limaico, J.E., Zúbelzu-Minguez, S., Rodríguez-Sinobas, L. 2022. Optimal irrigation scheduling for greenhouse tomato crop (*Solanum lycopersicum* L.) in Ecuador. *Agronomy* 12: 1020. doi.org/10.3390/agronomy12051020
- Coyago-Cruz, E., Corell, M., Moriana, A., Hernanz, D., Stinco, C.M., Mapelli-Brahm, P., Meléndez-Martínez, A.J. 2022. Effect of regulated deficit irrigation on commercial quality parameters, carotenoids, phenolics and sugars of the black cherry tomato (*Solanum lycopersicum* L.) ‘Sunchocola’. *J. Food Compos. Anal.* 105: 104220. doi.org/10.1016/j.jfca.2021.104220

- Dangwal, N.S., Patel, N.R., Kumari, M., Saha, S.K. 2016. Monitoring of water stress in wheat using multispectral indices derived from Landsat-TM. *Geocarto Int.* 31: 682–693. doi.org/10.1080/10106049.2015.1073369
- Du, Y., Cao, H., Liu, S., Gu, X., Cao, Y. 2017. Response of yield, quality, water and nitrogen use efficiency of tomato to different levels of water and nitrogen under drip irrigation in Northwestern China. *J. Integ. Agric.* 16: 1153–1161. doi.org/10.1016/S2095-3119(16)61371-0
- Dumas, Y., Dadomo, M., Di Lucca, G., Grolier, P. 2003. Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. *J. Sci. Food Agric.* 83: 369–382. doi.org/10.1002/jsfa.1370
- Farquhar, G.D., Sharkey, T.D. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Biol.* 33: 317–345. doi.org/10.1146/annurev.pp.33.060182.001533
- Fischer, G., Almanza-Merchán, P.J., Ramírez, F. 2012. Source-sink relationships in fruit species: a review. *Rev. Colomb. Cienc. Hortic.* 6: 238–253. dx.doi.org/10.17584/rcch.2012v6i2.1980
- Gamon, J.A., Peñuelas, J., Field, C.B. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic. *Remote Sens. Environ.* 41: 35–44. doi.org/10.1016/0034-4257(92)90059-S
- Gamon, J.A., Serrano, L., Surfus, J.S. 1997. The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia* 112: 492–501. doi.org/10.1007/s004420050337
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G. 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226: 1550–1566. doi.org/10.1111/nph.16485
- Guo, Y.P., Zhou, H.F., Zhang, L.C. 2006. Photosynthetic characteristics and protective mechanisms against photooxidation during high temperature stress in two citrus species. *Sci. Hortic.* 108: 260–267. doi: 10.1016/j.scienta.2006.01.029
- Hadi, J., Zein, K., Isam, B., Mustapha, H. 2017. Determining water requirements of biblical hyssop using an ET-based drip irrigation system. *Agric. Water Manag. Part A* 180: 107–117. doi.org/10.1016/j.agwat.2016.11.008
- Harmanto, Salokhe, V.M., Babel, M.S., Tantau, H.J. 2005. Water requirement of drip irrigated tomatoes grown in greenhouse in tropical environment. *Agric. Water Manag.* 71: 225–242. doi.org/10.1016/j.agwat.2004.09.003
- Hatfield, J.L., Dold, C. 2019. Water-use efficiency: Advances and challenges in a changing climate. *Front. Plant Sci.* 10: 103.1–103.14. doi.org/10.3389/fpls.2019.00103
- Hichem, H., Naceur, A.E., Mounir, D. 2009. Effects of salt stress on photosynthesis, PSII photochemistry and thermal energy dissipation in leaves of two corn (*Zea mays* L.) varieties. *Photosynthetica*. 47: 517–526. doi: 10.1007/s11099-009-0077-5
- Hott, M.O., Reis, E.F., Lima, V.L.S., Pereira, L.R., Garcia, G.O. 2018. Development of tomato plants under different water tensions in soil during the productive stage. *IDESIA (Chile)*. 36: 63–68.
- Ihuoma, S., Madramootoo, C. 2019a. Crop reflectance indices for mapping water stress in greenhouse grown bell pepper. *Agric. Water Manag.* 219: 49–58. doi.org/10.1016/j.agwat.2019.04.001
- Ihuoma, S., Madramootoo, C. 2019b. Sensitivity of spectral vegetation indices for monitoring water stress in tomato plants. *Comput. Electron. Agric.* 163: 104860.
- Jiang, M., Zhang, J. 2002. Water stress-induced abscisic acid accumulation triggers the increased generation of reactive oxygen species and up-regulates the activities of antioxidant enzymes. *J. Exp. Bot.* 53: 2401–2410. doi.org/10.1093/jxb/erf090
- Kabir, M.Y., Nambeesan, S.U., Bautista, J., Díaz-Perez, J.C. 2021. Effect of irrigation level on plant growth, physiology and fruit yield and quality in bell pepper (*Capsicum annuum* L.). *Sci. Hortic.* 281: 109902. doi: 10.1016/j.scienta.2021.109902
- Katsoulas, N., Angeliki, E., Konstantinos, F., Murat, K., Thomas, B., Constantinos, K. 2016. Crop reflectance monitoring as a tool for water stress detection in greenhouses: A review. *Biosyst. Eng.* 151: 374–398. doi.org/10.1016/j.biosystemseng.2016.10.003
- Kirkham, M.B. 2005. Field capacity, wilting point, available water, and the non-limiting water range. In: Kirkham, M.B. (Ed.). *Principles of Soil and Plant Water Relations*. Elsevier Inc. Amsterdam, the Netherlands, pp. 101–115.
- Li, B., Shukl, M.K., Du, T. 2021a. Combined environmental stresses induced by drip irrigation positively affect most solar greenhouse grown tomato fruit quality. *Sci. Hortic.* 288: 110334. doi: 10.1016/j.scienta.2021.110334
- Li, B., Wim, V., Shukla, M.K., Du, T. 2021b. Drip irrigation provides a trade-off between yield and nutritional quality of tomato in the solar greenhouse. *Agric. Water Manag.* 249: 106777. doi: 10.1016/j.agwat.2021.106777
- Li, X., Ye, J., Munir, S., Yang, T., Chen, W., Liu, G., Zheng, W., Zhang, Y. 2019. Biosynthetic gene pyramiding leads to ascorbate accumulation with enhanced oxidative stress tolerance in tomato. *Int. J. Mol. Sci.* 20: 1558. doi: 10.3390/ijms20071558
- Liu, H., Li, H., Ning, H., Zhang, X., Li, S., Pang, J., Wang, G., Sun, J. 2019. Optimizing irrigation frequency and amount to balance yield, fruit quality and water use efficiency of greenhouse tomato. *Agric. Water Manag.* 226: 105787. doi.org/10.1016/j.agwat.2019.105787
- Liu, H.R., Meng, F.L., Miao, H.Y., et al. 2018. Effects of postharvest methyl jasmonate treatment on main health-promoting components and volatile organic compounds in cherry tomato fruits. *Food Chem.* 263: 194–200. doi: 10.1016/j.foodchem.2018.04.124
- Maxwell, K., Johnson, G.N. 2000. Chlorophyll fluorescence-a practical guide. *J. Exp. Bot.* 51: 659–668. doi.org/10.1093/jexbot/51.345.659
- Melo, A.S., Suassuna, J.F., Fernandes, P.D., Brito, M.E.B., Suassuna, A.F., Netto, A.O.A. 2010. Vegetative growth, stomatal resistance, photosynthetic efficiency and yield of watermelon plants under different water levels. *Acta Sci. Agron.* 32: 73–79.
- Mialyk, O., Booij, M.J., Schyns, J.F., Berger, M. 2024. Evolution of global water footprints of crop production in 1990–2019. *Environ. Res. Lett.* 19: 114015. doi: 10.1088/1748-9326/ad78e9
- Munir, S., Liu, H., Xing, Y., Hussain, S., Ouyang, B., Zhang, Y., Li, H., Ye, Z. 2016. Overexpression of calmodulin-like (*ShCML44*) stress-responsive gene from *Solanum habrochaites* enhances tolerance to multiple abiotic stresses. *Sci. Rep.* 6: 31772. doi.org/10.1038/srep31772
- Munir, S., Mumtaz, M.A., Ahiakpa, J.K., et al. 2020. Genome-wide analysis of Myo-inositol oxygenase gene family in tomato reveals their involvement in ascorbic acid accumulation. *BMC Genomics* 21: 284. doi.org/10.1186/s12864-020-6708-8



- Nahar, K., Gretzmacher, R. 2002. Effect of water stress on nutrient uptake, yield and quality of tomato (*Lycopersicon esculentum* Mill.) under subtropical conditions. *Die Bodenkultur* 53: 45–51.
- Nemeskéri, E., Helyes, L. 2019. Physiological responses of selected vegetable crop species to water stress. *Agronomy* 9: 447. doi.org/10.3390/agronomy9080447
- Noh, H., Lee, J. 2022. The effect of vapor pressure deficit regulation on the growth of tomato plants grown in different planting environments. *Appl. Sci.* 12: 3667. doi.org/10.3390/app12073667
- Osakabe Y.K., Shinozaki, K., Tran, L.S.P. 2014. Response of plants to water stress. *Front. Plant Sci.* 5: 86. doi.org/10.3389/fpls.2014.00086
- Padmanabhan, P., Cheema, A., Paliyath, G. 2016. Solanaceous Fruits Including Tomato, Eggplant, and Peppers. University of Guelph. Guelph, ON, Canada
- Peñuelas, J., Filella, I., Biel, C., Serrano, L., Savé, R. 1993. The reflectance at the 950–970 nm region as an indicator of plant water status. *Int. J. Remote Sens.* 14: 1887–1905. doi.org/10.1080/01431169308954010
- Pereira, J.S., Kozlowsky, T.T. 1976. Leaf anatomy and water relations of *Eucalyptus camaldulensis* and *E. globulus* seedlings, *Canad. J. Bot.* 54: 2868–2880. doi.org/10.1139/b76-308
- Pernice, R., Parisi, M., Giodano, I., Pentangelo, A., Giulia, G., Gallo, M., Fogliano, V., Ritieni, A. 2010. Antioxidants profile of small tomato fruits: effect of irrigation and industrial process. *Sci. Hortic.* 126: 156–163. doi.org/10.1016/j.scienta.2010.06.021
- Resh, H.M. 2012. *Hydroponic Food Production: A Definitive Guidebook for the Advanced Home Gardener and the Commercial Hydroponic Grower*. CRC Press. Boca Raton, FL, USA. dx.doi.org/10.1201/b12
- Ritchie, J.T. 1998. Soil water balance and plant water stress. In: Tsuji, G.Y., Hoogenboom, G. and Thornton, P.K. (Eds). *Understanding Options for Agricultural Production*. Kluwer Academic Publishers. London, UK. pp. 41–54. doi: 10.1007/978-94-017-3624-4\_3
- Rodrigues, F., Sousa, B., Soares, C., Moreira, D., Pereira, C., Moutinho-Pereira, J., Cunha, A. Fidalgo, F. 2024. Are tomato plants co-exposed to heat and salinity able to ensure a proper carbon metabolism? – An insight into the photosynthetic hub. *Plant Physiol. Biochem.* 206: 108270. doi.org/10.1016/j.plaphy.2023.108270
- Santana, M.J., Vieira, T.A. 2010. Tomato response irrigated with different levels of soil water replacement. *Irriga.* 15: 443.
- Sato, S., Peet, M.M., Thomas, J.F. 2000. Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic, mild heat stress. *Plant Cell Environ.* 23: 719–726. doi.org/10.1046/j.1365-3040.2000.00589.x
- Smith, M.D., Sikka, A., Dirwai, T.L., Mabhaudhi, T. 2023. Research and innovation in agricultural water management for a water-secure world. *Irrig. Drain.* 72: 1245–1259. doi.org/10.1002/ird.2872
- Stamford, J.D., Vialet-Chabrand, S., Cameron, I., Lawson, T. 2023. Development of an accurate low cost NDVI imaging system for assessing plant health. *Plant Methods* 9: 9. doi.org/10.1186/s13007-023-00981-8
- Steudle, E. 2000. Water uptake by roots: Effects of water deficit. *J. Exp. Bot.* 51: 1531–1542. doi.org/10.1093/jexbot/51.350.1531
- Taiz, L., Zeigler, E. 2010. *Plant Physiology*. 5<sup>th</sup> edition, Oxford University Press. London, UK.
- Takebe, M., Yoneyama, T. 1995. An analysis of nitrate and ascorbic acid in crop exudates using a simple reflection photometer system. *JSSSPN* 66: 155–158.
- Tang, Z., Jin, Y., Alsina, M.M., McElrone, A.J., Bambach, N., Kustas, W.P. 2022. Vine water status mapping with multispectral UAV imagery and machine learning. *Irrig. Sci.* 40: 715–730. doi: 10.1007/s00271-022-00788-w
- Tigist, M., Workneh, T.S., Woldetsadik, K. 2013. Effects of variety on the quality of tomato stored under ambient conditions. *J. Food Sci. Technol.* 50: 477–486. doi: 10.1007/s13197-011-0378-0
- Wang, L., Li, Y., Zhang, X., Chen, K., Siddique, K.H.M. 2024. Soil water content and vapor pressure deficit affect ecosystem water use efficiency through different pathways. *J. Hydrol.* 640: 131732. doi: 10.1016/j.jhydrol.2024.131732
- Xu, S. Sun, X., Lu, H., Yang, H., Ruan, Q., Huang, H., Chen, M. 2018. Detecting and monitoring the flavor of tomato (*Solanum lycopersicum*) under the impact of postharvest handlings by physicochemical parameters and electronic nose. *Sensors* 18: 1847. doi.org/10.3390/s18061847
- Yu, G., Li, C., Zhang, L., et al. 2020. An allelic variant of *GAME9* determines its binding capacity with the *GAME17* promoter in the regulation of steroidal glycoalkaloid biosynthesis in tomato. *J. Exp. Bot.* 71: 2527–2536. doi: 10.1093/jxb/eraa014
- Yu, X., Niu, L., Zhang, Y., Xu, Z., Zhang, J., Zhang, S., Li, J. 2024. Vapour pressure deficit affects crop water productivity, yield, and quality in tomatoes. *Agric. Water Manag.* 299: 108879. doi.org/10.1016/j.agwat.2024.108879
- Yuan, X.K., Yang, Z.Q., Li, Y.X., Liu, Q., Han, W. 2016. Effects of different levels of water stress on leaf photosynthetic characteristics and antioxidant enzyme activities of greenhouse tomato. *Photosynthetica* 54: 28–39. doi.org/10.1007/s11099-015-0122-5
- Zhang, J., Wang, P., Ji, J., Long, H., Wu, X. 2021. Transcriptome analysis reveals the molecular mechanism of yield increases in maize under stable soil water supply. *PLOS ONE*. 16: e0257756. doi.org/10.1371/journal.pone.0257756