



Survival mode: physiological adjustments in tree tomato plants during flooding intensities and post-stress responses under shaded conditions

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Abstract

Key message A 4-day or more duration of flooding is considered a critical stress period for tree tomato plants, as they do not recover their plant water status, electron transport in photosystems, or growth during the post-stress period.

Abstract The tree tomato (*Solanum betaceum* Cav.) is a tropical fruit tree affected by climate variability, especially by flooding phenomena, which are projected to increase in the coming years, causing damage to the physiology and development of crops. Therefore, the objective of this research was to characterize the physiological response of the tree tomato in the vegetative stage under different days of flood duration (0, 2, 4, and 6 days) and later in the recovery period (14 days), in plants grown under controlled shade conditions. Stomatal conductance (g_s), leaf water potential (Ψ_{leaf}), leaf insertion angle, pigment concentration, chlorophyll *a* fluorescence, and plant growth were quantified. The results indicated that with 2 days of flooding, g_s , total chlorophyll concentration, root dry weight, and leaf area decreased slightly compared to the control. With 4 days of flooding, the plants showed more significant reductions in g_s and Ψ_{leaf} , which allowed the tree tomato to be classified as an isohydric plant. The 6-day flooding completely dehydrated the leaves. In addition, for the 4 and 6 days of flooding, the OJIP curves showed that the plants had lower photosynthetic efficiency, which was reflected in the reduction of the maximum photochemical quantum efficiency F_v/F_m , quantum yields, energy fluxes per reaction center, and linear electron flow (LEF). These parameters were more affected in the recovery period. The carotenoid concentration and non-photochemical dissipation Φ_{NPQ} increased as a photoprotective mechanism to dissipate excess energy. The biomass of the root and the aerial part decreased significantly as the intensity of the flooding increased. These results show that a time greater than or equal to 4 days of flooding with shade in tree tomato plants is considered a critical stress period.

Keywords Water status · Chlorophyll *a* fluorescence · Growth · Hypoxia · Waterlogging · *Solanum betaceum* · *Cyphomandra betacea*

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Introduction

The tree tomato or tamarillo (*Solanum betaceum* Cav.) is a tree species belonging to the Solanaceae family, originating from the mountains of the tropical Andes (Schotsmans et al. 2011). This crop grows naturally in Andean regions at elevations between 1000 and 3000 m above sea level, particularly in understory conditions, where it primarily benefits from diffuse radiation in shaded areas (Casierra-Posada et al. 2013; Ramírez and Kallarackal 2019). The consumption of its fruits offers various health benefits, including antioxidants, anti-obesity, anti-cancer, and prebiotic properties. Additionally, fruits exhibit antimicrobial and antifungal

activities that are valuable to the cosmetics and pharmaceutical industries (Diep et al. 2022).

Expanding and establishing the crop in new areas increase the risk of reduced production or yield due to adverse hydrometeorological phenomena (Ortiz-Bobea et al. 2021). Floods, which are projected to increase by 20% over the next 57 years due to global warming (Liu et al. 2023b), negatively impact crop development by causing soil waterlogging. In the tropical Andes, climate variability phenomena such as ENSO (El Niño-Southern Oscillation, specifically during the 'La Niña' phase) intensify the frequency of flooding and excessive rainfall. These conditions lead to oxygen deficiencies in Andean soils (Lopes et al. 2022), adversely affecting the growth and development of economically important tropical species, such as the tamarillo (Fischer et al. 2023). Furthermore, these phenomena are often accompanied by conditions of low radiation due to high cloud cover (Ren et al. 2023), exposing plants to combined stress from flooding and low light availability. Therefore, plant responses to flooding may be affected by low radiation under natural conditions.

Flooding stress negatively impacts plant physiology by reducing gas exchange, water relations, growth, and yield (Tian et al. 2021; Pan et al. 2021). Oxygen deficits in waterlogged soils force root cells into anaerobic metabolism, which decreases growth rates and root biomass accumulation (Dresbøll et al. 2013; Liu et al. 2023a). In tomato plants (*Solanum lycopersicum* L.), flooding reduces root hydraulic conductivity, leaf water potential, and transpiration within 12 h (Dell'Amico et al. 2001; Bhatt et al. 2015). This directly affects gas exchange and photosynthesis, leading to reduced stomatal conductance (Jackson et al. 2003), CO₂ assimilation, RuBisCO activity, electron transport, and photosystem II (PSII) functionality (de Pedro et al. 2020). Similarly, in eggplants subjected to flooding stress, reductions in leaf area, aboveground dry biomass, and leaf number have been observed (Sarker et al. 2023).

Shading or low solar radiation stress affects vital plant processes, such as photosynthesis and signaling in the molecular regulation of growth and development (Han et al. 2024). However, in some tropical Andean fruit trees that naturally grow in understories, shaded environments enhance growth, development, and photosynthetic performance, as reported in *Solanum quitoense* (Casierra-Posada et al. 2013) and *S. betaceum* (Li et al. 2023; Zheng et al. 2024). On the other hand, tropical Andean fruit trees of the Solanaceae family appear highly susceptible to flooding (Fischer et al. 2023). Flooding stress has been shown to reduce aboveground and root biomass, cause damage to PSII, accelerate chlorophyll degradation, and decrease relative water content in species, such as cape gooseberry (*Physalis peruviana* L.) (Villarreal-Navarrete et al. 2017), lulo (*Solanum quitoense* Lam.) (Sánchez-Reinoso et al. 2019; Flórez-Velasco et al. 2015; Cardona et al. 2016), and tree

tomato (Betancourt-Osorio et al. 2016). In fact, recent studies have highlighted the susceptibility of several commercial species of the genus *Solanum* to flooding stress, emphasizing the sensitivity of this group to waterlogged conditions (Gutiérrez-Villamil et al. 2025). Although susceptibility has been documented in tree tomato under 4-day flooding treatments applied at three different intervals (Betancourt-Osorio et al. 2016), information remains scarce regarding its physiological response to varying flooding durations (Gutiérrez-Villamil et al. 2025). Consequently, the minimum flooding period that *S. betaceum* can tolerate is still unknown.

The interaction of naturally occurring abiotic stress factors under field conditions, particularly flooding, shapes the phenotypic and genotypic responses of plants (Renziehausen et al. 2024). The combined effects of flooding and shade stress occur naturally in the field and can influence physiological responses depending on the species (Visser et al. 2016). In lulo trees (*Solanum quitoense*) grown in the Andean tropics, shading did not affect biomass production in response to flooding stress (Cardona et al. 2016); however, it did impact chlorophyll *a* fluorescence variable (Sánchez-Reinoso et al. 2019). Although the effects of flooding and shading have been studied in *Solanum quitoense*, little is known about how these stress factors interact in *S. betaceum*. Given its natural growth in shaded environments and its susceptibility to waterlogging, understanding how tree tomato plants respond to the combined effects of flooding and low radiation is essential for developing strategies to mitigate these stresses.

Understanding the physiological responses of tree tomato plants to different flooding durations is critical for developing breeding programs to mitigate the adverse effects of waterlogging (Liu et al. 2023b). Considering the productive potential of tree tomato in tropical and subtropical regions and the limited information available on Andean fruit trees under flooded conditions, this research aimed to characterize the physiological response of tree tomato plants in the vegetative stage under varying flooding durations (0, 2, 4, and 6 days) and during a subsequent recovery period (14 days) under controlled shade conditions. We tested the hypothesis that the physiological response of tree tomato to flooding depended on the duration of waterlogging under shaded conditions. We expected that increasing flooding duration would negatively impact plant growth, water relations, and photosynthetic capacity, even under low radiation, which resembled the natural conditions of this species during periods of excessive rainfall and high cloud cover.

Materials and methods

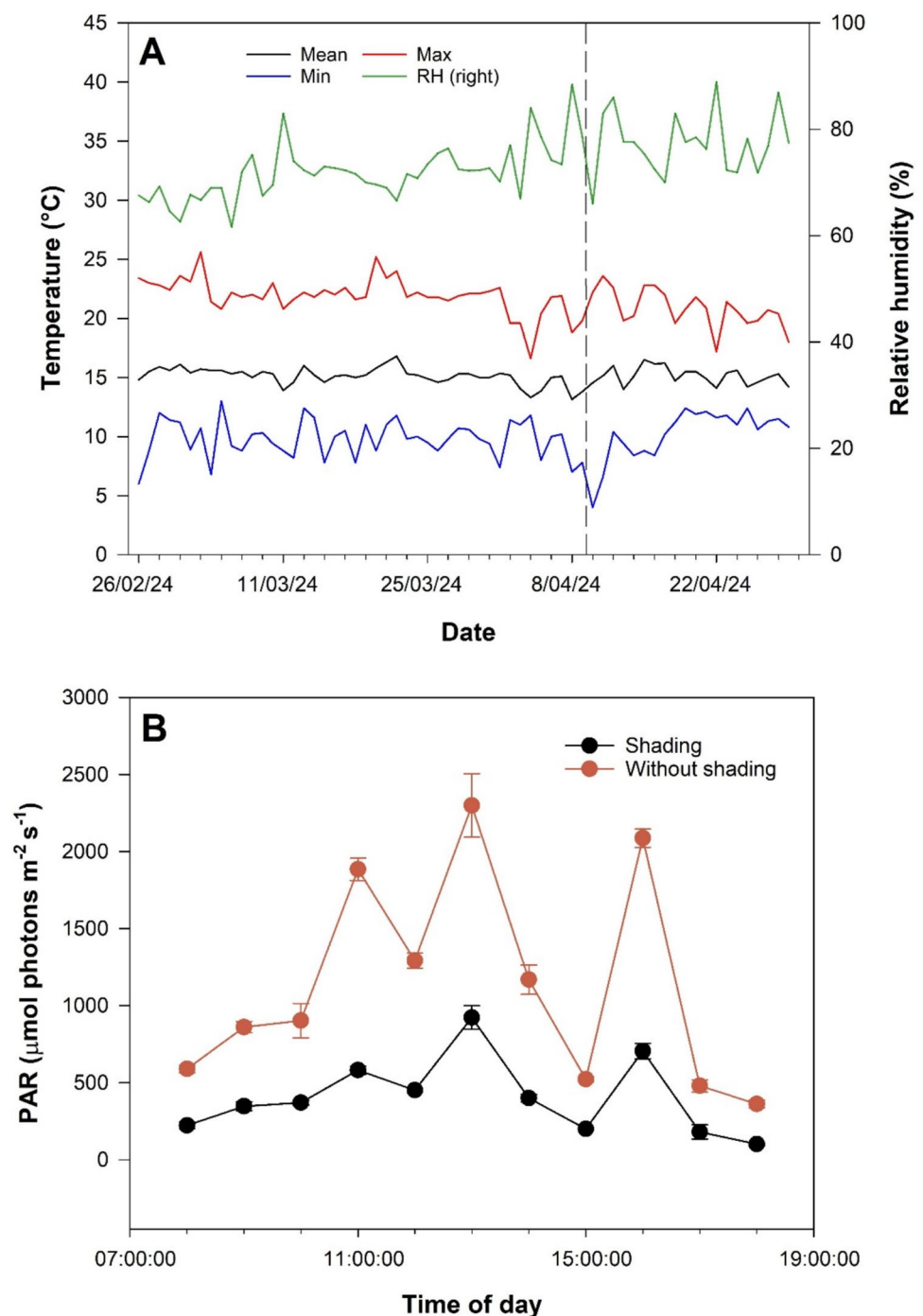
Experimental conditions and plant material

The study was carried out under field conditions at the experimental farm of the Universidad Pedagógica y Tecnológica de Colombia (2,787 m altitude; 5°33'97'' N, 73°21'32'' W) from February to April 2024. Field

environmental data during the experiment were obtained from the experimental farm's meteorological station (Fig. 1), where the mean temperature was 15.1 ± 0.73 °C, maximum 21.6 ± 1.63 °C, minimum 9.91 ± 1.78 °C, and average relative humidity $73.6 \pm 5.98\%$ (Fig. 1A).

Ten-month-old tree tomato plants (phenological stage 114a on the BBCH scale according to Acosta-Quezada et al. 2016) were transplanted into 30-L plastic bag pots containing black peat substrate with rice husks in a 3:1 ratio. Plants

Fig. 1 **A** Minimum, mean, and maximum temperatures and relative humidity during the experiment. **B** Photosynthetically active radiation (PAR) under shaded and unshaded field conditions. Vertical bars represent standard deviation ($n=5$). Data start at transplant. The vertical dashed line indicates the start of flooding treatments. Data end at the end of the experiment



were maintained at field capacity. Mineral nutrition was provided according to the requirements suggested by Bonnet and Cárdenas (2012) for 10-month-old tree tomato plants, adjusting it to Hoagland's solution (Betancourt-Osorio et al. 2016) with a liquid fertilizer (NutriponicVR, Walcoagro SA, Colombia) using a dose of 10 mL L⁻¹. A total of 150 mL of the nutrient solution was applied to each plant at the time of transplant and 21 days after transplant (DAT) (Betancourt-Osorio et al. 2016).

To simulate high cloudiness and low radiation conditions, plants were shaded 21 DAT until the end of flooding, using a high-density black polyethylene shade net that reduces 65% of light radiation. Photosynthetically active radiation (PAR) data on the leaf surface were obtained with the MultispecQ V2.0 sensor (PhotosynQ INC, MI, USA) (Kuhlgert et al. 2016) at the experiment site during a sunny day, to verify the average reduction at different hours of the day with and without polyshade (Fig. 1B). A group of plants was maintained under normal environmental conditions without polyshade or flooding, serving as the absolute control treatment (CK).

Flooding treatments

Once the plants had developed five fully expanded new leaves (46 DAT), the 75 tree tomato plants were randomly divided into five groups of 15 plants each. Each group corresponded to one of the flooding duration treatments evaluated: 0, 2, 4, and 6 days of flooding, plus an absolute control (CK), which was not subjected to flooding or shading, resulting in five treatments. The flooding durations were selected based on the findings of Betancourt-Osorio et al. (2016).

To induce root oxygen deficit (hypoxia), each pot was placed in a 30 L black plastic bag (caliber 8) to prevent water drainage. The pots were then saturated with water until the water table reached 5 cm above the substrate level. Flooding durations of 6, 4, and 2 days began at 43, 45, and 47 DAT, respectively, with the water table maintained at the designated level throughout the flooding period for each treatment. At 49 DAT, the bags were removed for all treatments, initiating a 14-day recovery period (ending at 63 DAT).

Quantified physiological parameters

Leaf water relations

Stomatal conductance (g_s) was measured between 11:00 a.m. and 1:00 p.m. on the fully developed fourth leaf from the apical zone, in accordance with the daily curve for this species (Supplementary Fig. 1). Measurements were performed using an SC-1 leaf porometer (Steady State Diffusion Porometer, Decagon Devices, Washington, USA). Leaf water potential at midday (Ψ_{leaf} , 12:00 p.m.) was estimated on the same leaves using a Schöllander pressure chamber

(Model 1000, PMS Instrument Co, Albany, OR, USA), following the methodology described by Toro-Tobón et al. (2022). Leaf angle was measured using the MultispecQ sensor, taking the 0° line between the horizontal base of the stem and the junction between the petiole and the stem (Kuhlgert et al. 2016). An increase in leaf angle indicated epinasty. These variables were assessed at the end of the flooding period for each treatment and again 14 days after the recovery period.

Leaf pigment concentration

Chlorophyll and carotenoid concentrations were measured 14 days after recovery in five leaves per treatment. To quantify leaf chlorophyll concentration, the protocols of Lichtenthaler (1987) and Solarte et al. (2010) were followed. A 0.1 g sample was taken from each plant's fifth fully developed leaf, without veins. The samples were ground with liquid nitrogen in a mortar, and chlorophyll pigments were extracted using 80% acetone under dark conditions to prevent photodegradation of the photosynthetic pigments. The concentrations of total chlorophyll, chlorophyll *a*, chlorophyll *b*, and carotenoids were determined by measuring absorbance at 645, 663, and 450 nm, respectively, using a Spectronic BioMate 3 UV-Vis spectrophotometer (Thermo, Madison, WI, USA).

Chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence was evaluated at two time points: at the end of the flooding period for each treatment and 14 days after recovery. Using the same leaves collected for chlorophyll concentration analysis, chlorophyll *a* fluorescence kinetics were assessed with the Pocket PEA unmodulated fluorometer (Hansatech Instruments Ltd, King's Lynn, Norfolk, UK) following the methodology of Toro-Tobón et al. (2022). The leaves were cut, placed in aluminum envelopes with damp absorbent paper to prevent dehydration, sealed in plastic bags, stored under cold conditions, and then transported to the laboratory between 6:00 a.m. and 8:00 a.m. Upon arrival, the leaves were further adapted to darkness for 30 min using specialized clips before measurements were taken. The light pulse lasted for 1 s at an intensity of 3,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photons. Data analysis was conducted using the fast-phase parameters of chlorophyll *a* fluorescence, obtained with the PEA Plus software (version 1.12, 2016), as described in Table 1. Additionally, chlorophyll *a* fluorescence induction curves (OJIP) and spider diagrams were generated using the ggplot2 library in RStudio (v. 2023.09.1–494). Spider diagrams presented data normalized to the control treatment, where a value of 1 was assigned to control plant data.

Table 1 The OJIP test parameters for the analysis of chlorophyll *a* fluorescence transient, as described by Strasser et al. (2000); Force et al. (2003); Bąba et al. (2016); Toro-Tobón et al. (2022)

Parameter	Physiological definition	Equation
V_J	Relative variable fluorescence at 2 ms (J-step)	$V_J = (F_J - F_o) / (F_o - F_o)$
V_I	Relative variable fluorescence at 30 ms (I-step)	$V_I = (F_I - F_o) / (F_m - F_o)$
F_v/F_m (Φ_{Po})	Maximum potential efficiency of PSII	$F_v/F_m = (F_m - F_o) / F_m$
Ψ_{Eo} (Ψ_o)	Efficiency with which a trapped exciton can move an electron after reduction of quinone (QA-)	$\Psi_{Eo} = 1 - V_J$
Φ_{Eo}	Probability that an absorbed electron moves an electron after QA-. Quantum yield for electron transport from QA- to plastoquinone (PQ)	$\Phi_{Eo} = (1 - F_o/F_m) * (1 - V_J)$
Φ_{Ro}	Quantum yield with which absorbed light energy (ABS) is used for the reduction of final electron acceptors on the acceptor side of PSI (RE), such as ferredoxin and NADP	$\delta Ro = \frac{RE_o}{ABS} = \left(1 - \frac{F_I}{F_m}\right) * (1 - V_J)$
δRo	Relative probability that an electron, once transferred beyond QA (ET), actually reaches the final acceptors on the acceptor side of PSI (RE)	$\delta Ro = RE_o/ET_o = (1 - V_I) / (1 - V_J)$
ABS/RC	Relationship between photon flux absorbed by antenna pigments and PSII reaction center (RC) chlorophyll (antenna size indicator for PSII)	$ABS/RC = (M_o/V_J) / [1 - (F_o/F_m)]$
DI_o/RC	Untrapped energy dissipation (DI) flux by RC at time 0	$DI_o/RC = (ABS/RC) - (TR_o/RC)$
TR_o/RC	Trapped energy (TR) flux from PSII by RC at time 0	$\frac{TR_o}{RC} = M_o * (1 - V_J) = \Phi_{Po} * \frac{ABS}{RC}$
ET_o/RC	Electron transport (ET) flux by RC at time 0	$\frac{ET_o}{RC} = M_o * (1 - V_J) * \Psi_{Eo} = \Psi_{Eo} * \frac{TR_o}{RC}$
RE_o/RC	Final electron acceptor reduction on the electron acceptor side of PSI (RE) at time 0 by RC	$\frac{RE_o}{RC} = M_o * (1 - V_J) * \Psi_{Eo} * \delta Ro$
PI_{ABS}	Multiparameter photosynthetic performance index expressing energy conservation from light absorption by PSII antenna complexes to electron transport to intersystem electron acceptors	$PI_{ABS} = \left(\frac{RC}{ABS}\right) * \left[\frac{\Phi_{Po}}{1 - \Phi_{Po}}\right] * \left[\frac{\Psi_{Eo}}{1 - \Psi_{Eo}}\right]$

The light-adapted phase of chlorophyll *a* fluorescence was evaluated using the MultispecQ V2.0 modulated fluorometer (<https://photosynq.com>) with the RIDES 2.0 protocol (Kuhlgert et al. 2016). This protocol was modified to use a constant PAR of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photons (RIDES 2.0 Mod). The operational quantum yield of photosystem II (Φ_{PSII}), linear electron flux (LEF), the quantum yield of regulated non-photochemical energy loss in PSII (Φ_{NPQ}), and quantum yield of non-regulatory energy dissipation (Φ_{NO}) were measured (Tietz et al. 2017).

Morphological traits of the plant

At the end of the treatment recovery period, various morphological traits were assessed, including leaf area, leaf dry weight (LDW), stem dry weight (SDW), shoot dry weight (STDW), root dry weight (RDW), total dry weight (TDW), and the shoot/root ratio (S:R). Leaf area was quantified using photographs with a known reference area, and analyzed with ImageJ® v. 1.54j software (National Institutes of Health, WI, USA), following the methodology described by Martin et al. (2020). Total biomass was estimated by drying plant organs (leaf, stem, and root) in an oven at 75 °C for 72 h (Sarker et al. 2023). The shoot/root ratio was calculated by dividing the shoot dry mass by the root dry mass.

Experimental design and statistical analysis

A completely randomized design was employed with a single factor: the duration of flooding in tree tomato plants (0, 2, 4, and 6 days). The four treatments consisted of five replicates, each containing three plants, for a total of 15 plants per treatment and 60 plants in the entire experiment. Data analysis was conducted using the nonparametric Kruskal–Wallis test for each response variable. Treatment medians were compared using the Dwass–Steel–Critchlow–Flinger (DSCF) pairwise comparison test ($p < 0.05$). The values presented in the graphs correspond to the median of the data. A Pearson correlation test was also performed between stomatal conductance and leaf water potential. All analyses were conducted in R software version 4.3.0. Graphs were created using the ggplot2 library version 3.4.2 (Wickham 2016) and SigmaPlot software version 14.0.0.124 (San José, CA: Systat Software, Inc.).

Results

Plant water relations

The water status of tree tomato plants was significantly affected as the duration of flooding increased (Fig. 2).

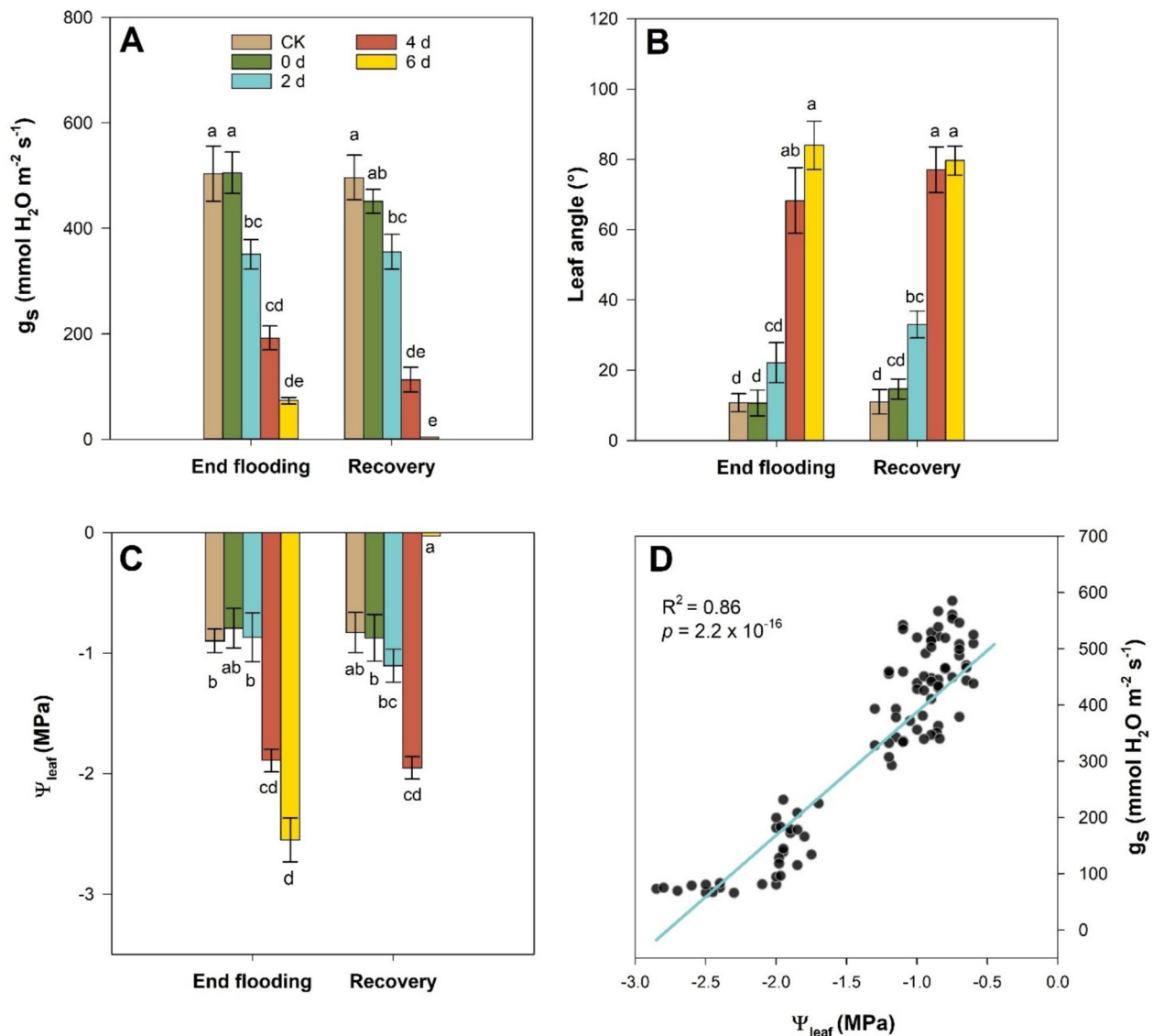


Fig. 2 **A** Stomatal conductance (g_s), **B** leaf angle relative to the horizontal baseline, and **C** leaf water potential at noon (Ψ_{leaf}) in tree tomato plants subjected to 0, 2, 4, and 6 days of flooding under shade

conditions, as well as in the CK treatment (no flooding and no shading), measured at the end of the stress period and 14 days after recovery. **(D)** Pearson linear correlation analysis between g_s and Ψ_{leaf}

Plants without waterlogging and shading (CK) showed similar values in stomatal conductance (g_s) and leaf angle to the treatment without flooding but with shading (0 d); however, leaf water potential at midday (Ψ_{leaf}) showed lower values in CK. At the end of the stress period, g_s decreased statistically significantly ($p < 0.0001$) by 30.5% ($348.8 \text{ mmol m}^{-2} \text{s}^{-1} \text{H}_2\text{O}$), 61.9% ($182.2 \text{ mmol m}^{-2} \text{s}^{-1} \text{H}_2\text{O}$), and 85.5% ($73.9 \text{ mmol m}^{-2} \text{s}^{-1} \text{H}_2\text{O}$) after 2, 4, and 6 days of flooding, respectively, compared to non-flooded plants (0 d, $505.7 \text{ mmol m}^{-2} \text{s}^{-1} \text{H}_2\text{O}$) (Fig. 2A). During the recovery period, the g_s of plants flooded for 4 days continued to decrease by 75% ($116.6 \text{ mmol m}^{-2} \text{s}^{-1} \text{H}_2\text{O}$).

Plants flooded for 6 days did not register g_s values, because their leaves were dead.

The Ψ_{leaf} showed reductions of 138.3% and 221.2% compared to the control (0 d) in plants flooding for 4 and 6 days, respectively (Fig. 2C). After the recovery period, the flooded plants maintained their Ψ_{leaf} values, except for those in the 6-day flooding treatment, which did not register values due to leaf dehydration and death.

The variables g_s and Ψ_{leaf} showed a high correlation ($R = 0.86$, $p = 2.2 \times 10^{-16}$) according to Pearson analysis (Fig. 2D), indicating limitations in water uptake and transport in flooded plants. Values for g_s and Ψ_{leaf} from the 6-day

flooding treatment, which could not be recorded due to leaf death (marked as 0 in Fig. 2A, C), were excluded from the linear correlation analysis. Leaf angle increased as the flooding duration extended (Fig. 2B) and showed a slight increase during the recovery period in plants subjected to 2- and 4-day flooding treatments.

Error bars represent the standard deviation ($n = 15$). Different letters above bars indicate statistical differences in the interaction between treatments and measurement times, as determined by the Kruskal–Wallis test ($p < 0.05$). Leaf angle values increased, because the horizontal line was used as the baseline reference.

Leaf pigment concentration

Leaf coloration in tree tomato plants was visibly affected by the duration of flooding (Fig. 3). Plants subjected to 2 and 4 days of flooding exhibited light green and yellow coloration, respectively, compared to the dark green leaves of the control plants. Leaves exposed to 6 days of flooding displayed a black–purple hue distributed across the entire leaf blade.

The concentrations of chlorophyll *a*, total chlorophyll, and carotenoids showed significant statistical differences between treatments (Table 2). However, the concentration of chlorophyll *b* did not exhibit statistical differences among the flooding treatments, maintaining an average value of $0.38 \pm 0.18 \text{ mg g}^{-1}$. Plants without flooding and without shade (CK) showed lower values in chlorophyll *a* and total chlorophyll concentration compared to plants without flooding, but with shade (0 d). In contrast, flooding for 2 and 4 days reduced the concentrations of chlorophyll *a* and total chlorophyll in tree tomato leaves compared to the control, which aligned with the observed visual appearance of the leaves. Interestingly, plants subjected to 6 days of flooding did not display significant differences in these parameters compared to non-flooded plants. Additionally, carotenoid concentrations increased by 23.5% and 100% following 4 and 6 days of flooding, respectively.

The chlorophyll *a/b* ratio varied among treatments (Table 2). The CK and 0-day flooding treatments showed similar values. The highest values were observed during the 2 and 6 days of flooding. In contrast, the 4-day flooding treatment had the lowest ratio.

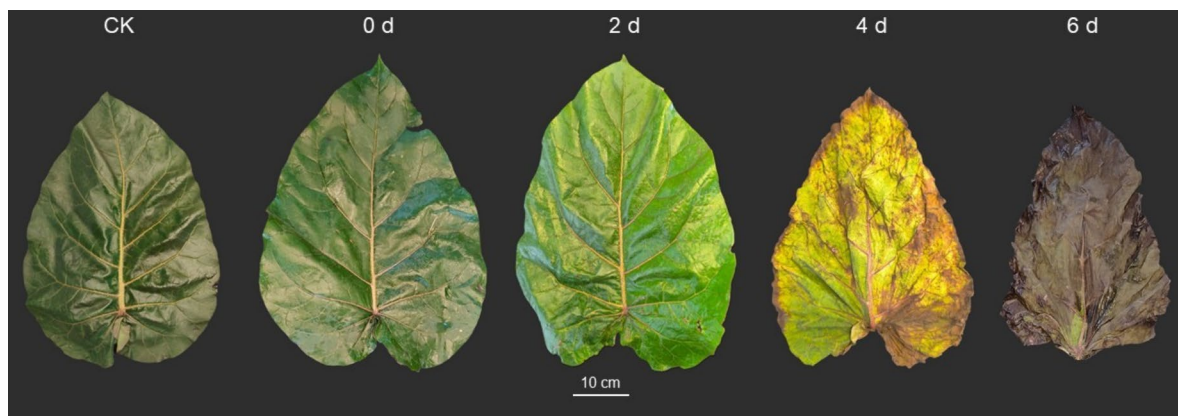


Fig. 3 Visual appearance of tree tomato leaves subjected to 0, 2, 4, and 6 days of flooding under shaded conditions, as well as in the CK treatment (no flooding and no shading). Representative leaves of each treatment were collected 14 days after recovery from stress

Table 2 Chlorophyll and carotenoid concentrations in tree tomato leaves subjected to varying durations of flooding under shaded conditions

Flood intensities (days)	Chlorophyll <i>a</i> (mg g^{-1})*	Chlorophyll <i>b</i> (mg g^{-1})	Chlorophyll <i>a/b</i> ratio	Total chlorophyll (mg g^{-1})	Carotenoids (mg g^{-1})
CK	0.47 ± 0.04 b	0.45 ± 0.13 ns	1.07 ± 0.17 d	0.89 ± 0.19 ab	0.15 ± 0.02 b
0	0.58 ± 0.16 ab	0.49 ± 0.2 ns	1.27 ± 0.39 c	1.10 ± 0.25 a	0.17 ± 0.03 b
2	0.44 ± 0.03 bc	0.25 ± 0.14 ns	2.15 ± 0.29 b	0.79 ± 0.13 ab	0.13 ± 0.02 b
4	0.38 ± 0.10 c	0.37 ± 0.14 ns	1.02 ± 0.47 d	0.59 ± 0.21 b	0.21 ± 0.13 ab
6	0.87 ± 0.34 a	0.29 ± 0.16 ns	2.44 ± 0.40 a	1.16 ± 0.29 a	0.34 ± 0.13 a

*Expressed in grams of fresh mass. Samples were collected 14 days after recovery from stress. $\pm$ represents the standard deviation ($n = 5$)

Different letters between rows indicate statistical differences in flooding intensity according to the Kruskal–Wallis test ($p < 0.05$)

Chlorophyll *a* fluorescence

Figures 4 and 5 present the parameters obtained from the fast phase of chlorophyll *a* fluorescence emission for tree tomato plants subjected to varying flooding durations. The maximum quantum efficiency of PSII (F_v/F_m), the performance index (PI_{ABS}), the linear electron flux (LEF), and the effective quantum yield of PSII (Φ_{PSII}) exhibited lower values at the end of the stress period and 14 days after recovery in plants flooded for 4 and 6 days compared to those flooded for 0 and 2 days (Fig. 4A–C). This reduction was more pronounced during the recovery period. Conversely, the regulated energy dissipation quantum efficiency in PSII (Φ_{NPQ}) increased with longer flooding durations (Fig. 4F), reaching its highest values during recovery. In contrast, the non-regulated energy dissipation quantum efficiency (Φ_{NO}) decreased as flooding duration increased (Fig. 4E). Furthermore, the plants in the CK treatment showed lower values than the plants without flooding and with shading (0 d) in the F_v/F_m , PI_{ABS} , LEF, and Φ_{PSII} .

Error bars represent standard deviation ($n = 15$). Different lowercase letters between bars indicate statistical differences in the interaction of treatments and measurement times according to the Kruskal–Wallis test ($p < 0.05$).

The OJIP curves at the end of stress (Fig. 5A) showed similar behavior from stage O to I (30 ms). However, at stage P (1 s), plants flooded for 6 days exhibited less pronounced peaks, corresponding to a gradual decrease in fluorescence intensity. During the recovery period (Fig. 5C), plants subjected to 4 days of flooding displayed higher fluorescence values between stages O and J (2 ms), but with lower peaks at stage P. Plants flooded for 6 days demonstrated an abrupt decrease, and the fluorescence emission kinetics revealed a K phase between stages O and J, resulting in the absence of a complete JIP curve (Fig. 5C). The plants of the CK and 0 d control treatments showed similar OJIP curves.

The shaded region represents the standard error ($n = 15$). The vertical dashed lines in the OJIP curves indicate O-fluorescence intensity recorded at F_o (50 μ s), J: 2 ms, I: 30 ms, and P: maximum fluorescence intensity (F_m) at 1 s. The values of the spider diagrams are normalized with respect to the control treatment (CK).

The electron quantum yields (Ψ_{Eo} , ϕ_{Eo} , ϕ_{Ro} , and δRo) were reduced in plants flooded for 4 and 6 days compared to those flooded for 0 and 2 days, and CK (Table 3), both at the end of stress (Fig. 5B) and after recovery (Fig. 5D). This reduction was more pronounced at the end of the recovery period. Additionally, energy fluxes within the leaf showed increased values for energy absorption (ABS), dissipation (DI), and trapped energy (TR) per reaction center in plants flooded for 4 and 6 days. Consequently, the energy available for electron transport (ET) and the final reduction of electrons in PSI (RE) were reduced, while the relative

variable fluorescence values increased in V_j and V_i (Table 3, Fig. 5B–D). For plants subjected to 2 days of flooding, energy fluxes and electron transport did not significantly differ from the control.

Plant morphological traits

The leaf, stem, root dry weights, and leaf area of tree tomato plants decreased as the flooding duration increased (Table 4). The RDW decreased by 50.6%, 71.4%, and 85.7% in plants subjected to 2, 4, and 6 days of flooding, respectively, compared to the control (0 d). This indicates a significant negative effect of flooding on root development, which led to an increase in the S:R ratio with longer flooding durations.

The STDW also decreased as flooding duration increased, resulting in reduced leaf growth and increased leaf abscission. Similarly, the leaf area of the plants decreased by 24.5%, 68.4%, and 82.5% for plants flooded for 2, 4, and 6 days, respectively. These findings suggest that under shaded conditions, water limitation, photoinhibition, chlorophyll degradation, and poor photosynthetic performance during 4 or more days of flooding significantly reduced tree tomato root growth and leaf area.

RDW Root dry weight, SDW stem dry weight, LDW leaf dry weight, STDW Shoot dry weight, TDW Total dry weight, S:R shoot:root ratio

*The samples were taken after 14 days of stress recovery. $\pm$ represents the standard deviation ($n = 15$). Different letters within columns indicate statistical differences in flooding intensity according to the Kruskal–Wallis test ($p < 0.05$)

Discussion

Soil re-oxygenation affects physiological responses

The plant response during the recovery phase after flooding has often been overlooked (Jiménez et al. 2024). Rapid recovery following the removal of root hypoxia is a critical factor in stress tolerance, as a network of signals controlling water loss and senescence plays a significant role in influencing recovery after prolonged submersion (Yeung et al. 2018). In tree tomato plants, only a slight recovery in water-related variables (g_s and Ψ_{leaf}) and chlorophyll fluorescence was observed after 2 days of flooding; however, a reduction in biomass accumulation was noted. In contrast, plants that flooded for 4 and 6 days did not exhibit recovery in the analyzed variables. On the contrary, these variables often showed further decline. This can be attributed to the increased formation of reactive oxygen species (ROS) and toxic byproducts of fermentative metabolism during root re-oxygenation due to the sudden high concentration of O_2

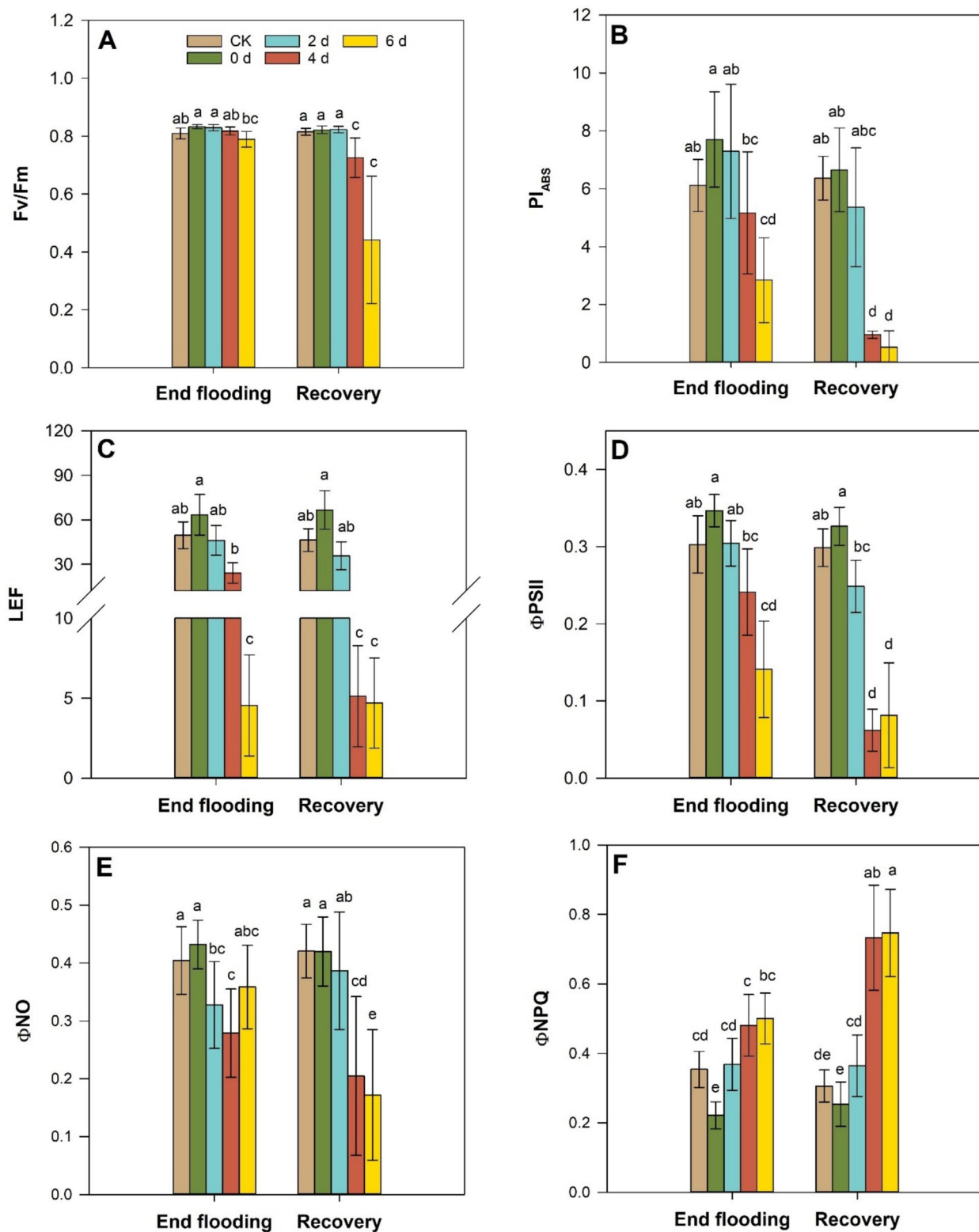


Fig. 4 **A** Maximum quantum efficiency of PSII (F_v/F_m), **B** vitality index (PI_{ABS}), **C** linear electron flux (LEF), **D** effective quantum yield of photosystem II (Φ_{PSII}), **E** quantum yield of unregulated energy dissipation (Φ_{NO}), and **F** quantum yield of regulated non-photo-

chemical energy loss in PSII (Φ_{NPQ}) in tree tomato leaves subjected to 0, 2, 4, and 6 days of flooding, as well as in the CK treatment (no flooding and no shading), measured at the end of stress and 14 days after recovery

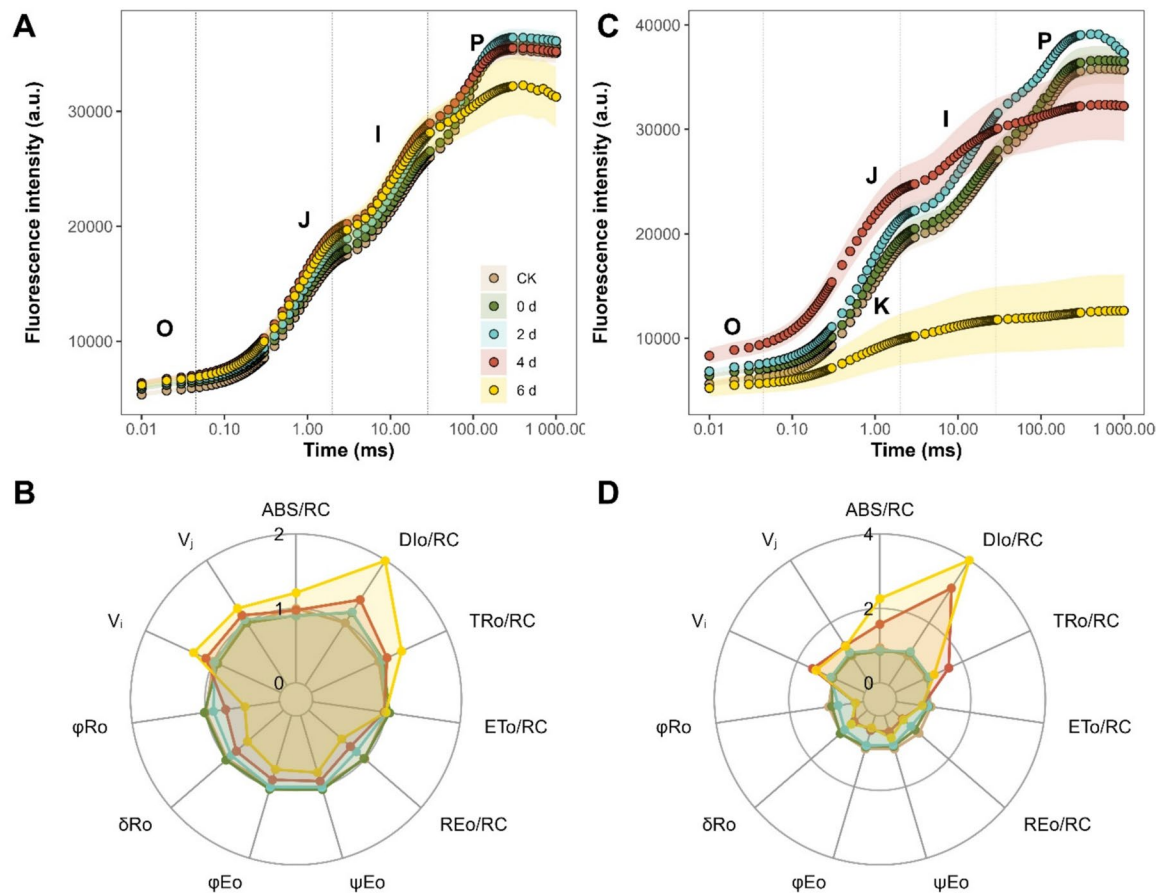


Fig. 5 The OJIP transient curves and spider diagrams of parameters obtained from the fast emission phase of chlorophyll *a* fluorescence in tree tomato leaves subjected to 0, 2, 4, and 6 days of flooding, as

well as in the CK treatment (no flooding and no shading), at the end of the stress (**A, B**) and at 14 days of recovery (**C, D**)

, which accelerates plant senescence (Jethva et al. 2022). In this context, tree tomato is considered a species highly susceptible to flooding stress (Betancourt-Orsorio et al. 2016). Our research determined that tree tomato plants do not show significant reconditioning of their physiological attributes during recovery when subjected to 4 or more days of flooding.

Increased flooding duration affects plant water balance

Stomatal conductance (g_s) and leaf water potential at midday (Ψ_{leaf}) are plant water status variables that are influenced by flooding stress, as reported in the other studies (Horchani et al. 2008; Else et al. 2009; de Pedro et al. 2020). This study observed a decrease in g_s and Ψ_{leaf} as the flooding duration increased. This is because the roots send a hydraulic signal that reduces water flow (Else et al. 2009), which triggers stomatal closure mediated by abscisic acid (ABA) and ethylene (Striker et al. 2017), to prevent water loss through transpiration. During flooding, ethylene accumulation in the

aerial parts of the plant results from 1-aminocyclopropane-1-carboxylate (ACC) transport from the roots, where low oxygen levels prevent its conversion to ethylene. Once in the leaves, ACC interacts with O_2 , producing high ethylene concentrations (Pita et al. 2023; Chen et al. 2024).

Furthermore, a strong correlation was observed between the reduction in stomatal conductance and leaf water potential, suggesting that tree tomato plants could be classified as an isohydric species. This indicates that the plant tightly regulates its leaf water potential, rapidly closing the stomata in response to stress-induced leaf dehydration (Hochberg et al. 2018).

Leaf epinastic movement has been associated with flooding stress in plants, as it can indicate leaf dehydration and the role of ethylene within the plant (Geldhof and Novák 2024). The epinastic curvature observed in the leaves of tree tomato plants (Fig. 2B) can be explained by ethylene's role as a mediator of adaptive responses to flooding stress (Perata 2020; Else et al. 1995; Geisler-Lee et al. 2010). According to the model proposed by Geldhof

Table 3 Parameters obtained from the fast emission phase of chlorophyll *a* fluorescence

Parameter*	Moment	CK		Treatment		
			0 d	2 d	4 d	6 d
V_J	End of flood	0.40 ± 0.05 cd	0.37 ± 0.02 d	0.39 ± 0.04 cd	0.45 ± 0.05 bc	0.52 ± 0.13 ab
	Recovery	0.42 ± 0.05 cd	0.42 ± 0.05 cd	0.45 ± 0.06 bc	0.69 ± 0.12 a	0.65 ± 0.12 a
V_I	End of flood	0.67 ± 0.02 e	0.69 ± 0.04 e	0.72 ± 0.03 cde	0.77 ± 0.04 bc	0.85 ± 0.05 a
	Recovery	0.68 ± 0.04 e	0.71 ± 0.06 de	0.75 ± 0.04 bcd	0.92 ± 0.05 ab	0.91 ± 0.04 a
Ψ_{Eo}	End of flood	0.60 ± 0.05 a	0.62 ± 0.02 a	0.61 ± 0.04 a	0.55 ± 0.05 bc	0.48 ± 0.06 cd
	Recovery	0.62 ± 0.06 a	0.57 ± 0.05 a	0.55 ± 0.06 ab	0.30 ± 0.12 d	0.42 ± 0.06 d
Φ_{Eo}	End of flood	0.50 ± 0.04 ab	0.52 ± 0.02 a	0.50 ± 0.04 ab	0.45 ± 0.05 bc	0.38 ± 0.06 cd
	Recovery	0.51 ± 0.03 ab	0.47 ± 0.05 ab	0.45 ± 0.06 abc	0.22 ± 0.11 d	0.19 ± 0.08 d
δRo	End of flood	0.48 ± 0.06 a	0.49 ± 0.06 a	0.45 ± 0.03 ab	0.40 ± 0.04 bc	0.31 ± 0.06 cd
	Recovery	0.49 ± 0.06 a	0.51 ± 0.08 a	0.42 ± 0.03 ab	0.24 ± 0.1 d	0.30 ± 0.11 d
ΦRo	End of flood	0.25 ± 0.04 a	0.26 ± 0.03 a	0.23 ± 0.03 ab	0.18 ± 0.04 bc	0.12 ± 0.04 cd
	Recovery	0.26 ± 0.04 a	0.24 ± 0.05 a	0.19 ± 0.03 b	0.06 ± 0.04 d	0.06 ± 0.03 d
ABS/RC	End of flood	1.11 ± 0.18 d	1.09 ± 0.09 d	1.09 ± 0.09 d	1.18 ± 0.17 cd	1.46 ± 0.35 bc
	Recovery	1.14 ± 0.17 d	1.12 ± 0.11 d	1.15 ± 0.13 d	2.08 ± 0.5 ab	2.98 ± 1.17 a
DI_0/RC	End of flood	0.19 ± 0.04 d	0.18 ± 0.02 d	0.18 ± 0.03 d	0.22 ± 0.05 cd	0.31 ± 0.12 bc
	Recovery	0.18 ± 0.04 d	0.20 ± 0.03 d	0.21 ± 0.04 d	0.59 ± 0.26 ab	1.90 ± 1.26 a
TR_0/RC	End of flood	0.86 ± 0.09 d	0.91 ± 0.07 d	0.90 ± 0.07 d	0.96 ± 0.13 bcd	1.15 ± 0.24 ab
	Recovery	0.88 ± 0.08 d	0.92 ± 0.08 d	0.94 ± 0.09 cd	1.48 ± 0.27 a	1.08 ± 0.23 bc
ET_0/RC	End of flood	0.54 ± 0.06 a	0.57 ± 0.04 a	0.54 ± 0.02 ab	0.53 ± 0.03 ab	0.54 ± 0.05 ab
	Recovery	0.57 ± 0.05 a	0.53 ± 0.07 ab	0.51 ± 0.05 b	0.43 ± 0.15 bc	0.43 ± 0.06 b
RE_0/RC	End of flood	0.29 ± 0.05 a	0.28 ± 0.05 a	0.24 ± 0.02 ab	0.21 ± 0.02 bc	0.17 ± 0.04 cd
	Recovery	0.31 ± 0.04 a	0.26 ± 0.05 ab	0.22 ± 0.030 bc	0.12 ± 0.07 d	0.13 ± 0.05 d

*Relative variable fluorescence at 2 ms (V_J) and 30 ms (V_I), quantum efficiencies (Ψ_{Eo} , Φ_{Eo} , δRo , ΦRo), and reaction center-specific energy flux parameters (ABS/RC, DI_0/RC , TR_0/RC , ET_0/RC , and RE_0/RC). $\pm$ represents the standard deviation ($n = 15$). Different letters within columns indicate statistical differences in flooding intensity according to the Kruskal–Wallis test ($p < 0.05$)

Table 4 Morphological traits and growth in tree tomato plants subjected to different intensities of flooding with shade

Variable	Flood intensities (days)*				
	CK	0	2	4	6
RDW (g)	46.77 ± 6.94 a	47.89 ± 11.16 a	23.65 ± 4.53 b	15.85 ± 3.41 bc	6.83 ± 1.34 c
SDW (g)	45.49 ± 4.13 a	46.01 ± 8.57 a	46.57 ± 7.35 a	34.02 ± 3.51 b	24.40 ± 5.22 b
LDW (g)	23.69 ± 3.70 ab	30.27 ± 6.37 a	22.45 ± 8.36 ab	14.98 ± 3.98 bc	8.66 ± 2.75 c
STDW (g)	69.17 ± 7.78 ab	76.28 ± 13.34 a	69.02 ± 15.58 ab	49.01 ± 7.03 bc	33.06 ± 7.67 c
TDW (g)	115.94 ± 7.87 a	124.17 ± 18.76 a	92.67 ± 19.69 b	64.84 ± 7.97 c	39.89 ± 7.48 c
S:R ratio	1.52 ± 0.36 b	1.65 ± 0.47 b	2.02 ± 0.30 ab	3.20 ± 0.74 a	5.01 ± 1.64 a
Leaf area (cm ²)	3986.1 ± 211.2 ab	4645.3 ± 919.1 a	3506.7 ± 588.9 b	1468.5 ± 186.1 c	814.7 ± 183.9 c

and Novák (2024), ethylene, together with ABA accumulated under hypoxia, acts on the leaf tissues of the petiole, promoting differential growth between the cells on the upper and lower sides, which causes leaf epinasty. Therefore, tree tomato plants exhibit this characteristic after four days of flooding, and ethylene likely plays a key role in signaling epinasty in this species.

The Increase in flooding duration alters the concentration of pigments in the leaf

The loss of coloration and the decrease in the concentration of chlorophyll *a* and total chlorophyll were evident in plants subjected to flooding for 2 and 4 days. Chlorophyll degradation is one of the most apparent physiological responses to flooding in many plants' sensitive to this stress (Pan et al.

2021), a response also observed in *Solanum quitoense* plants subjected to flooding (Flórez-Velasco et al. 2015). This degradation results from oxidative damage caused by reactive oxygen species (ROS) in the chloroplast, which cannot be regulated due to the reduced CO₂ assimilation caused by stomatal closure (Zeng et al. 2021). Furthermore, the large accumulation of ethylene due to flooding could signal senescence mechanisms in tree tomato leaves, such as chlorophyll degradation (Pita et al. 2023).

In contrast, plants subjected to 6 days of flooding did not show significant changes in chlorophyll concentration, and the leaves exhibited a black–purple coloration (Table 2, Fig. 3). The black–purple coloration may result from anthocyanin accumulation as a protective response to oxidative stress caused by flooding, as observed in tomato (Wen et al. 2024) and other tree species (Zhang et al. 2023). Similarly, the increase in carotenoids after 6 days of flooding could aid in photoprotection by dissipating excess energy and reducing oxidative damage (Pan et al. 2021). In contrast, the rise in chlorophyll *a* under abiotic stress is less documented and appears to be species-dependent, as seen in potato (Ramírez et al., 2014). These findings are unique to this treatment and require further study to clarify their role in combined stress responses.

The chlorophyll *a*, *b*, and total chlorophyll values found in this study were higher than those reported by Ramírez-Soler et al. (2021) for tree tomato leaves. This difference may be attributed to the fact that flooding was conducted under shaded conditions, simulating extreme rainfall and cloudiness (Fig. 1B). Shading may also influence the chlorophyll *a/b* ratio. In tomatoes, for instance, low radiation has been shown to increase chlorophyll *a* content without affecting chlorophyll *b* levels (Formisano et al. 2022), a trend similar to what was observed in non-flooded tree tomato plants (CK and 0 d). In this experiment, plants without flooding and without shade exhibited lower chlorophyll *a* and total chlorophyll levels than those exposed to shading, suggesting that shade promotes chlorophyll synthesis and accumulation in tree tomato plants. A similar effect was reported by Li et al. (2023), who found that a 50% reduction in natural light decreased the chlorophyll *a/b* ratio in tree tomato seedlings, consistent with our findings.

This increase in chlorophyll and carotenoid concentrations under shaded conditions is likely a physiological adaptation to maximize light capture in low-light environments, as shade has been shown to enhance the expression of genes involved in chlorophyll and carotenoid biosynthesis (Han et al. 2023). Therefore, shading in tree tomato may increase pigment concentration, potentially influencing tolerance to flooding stress. In lulo plants, the combination of shade and flooding stress was found to reduce electrolyte leakage and maintain chlorophyll content, improving tolerance to waterlogging (Sánchez-Reinoso et al. 2019). This effect may be

attributed to reduced photoinhibition under low-light conditions, which helps mitigate the negative impact of stomatal closure during flooding.

The carotenoid concentration increased as the flooding duration increased (Table 2). Carotenoids are crucial in protecting photosystems during oxidative stress by preventing ROS generation and dissipating excess absorbed energy as heat. This is considered an adaptive response to flooding stress (Pan et al. 2021). In this sense, tree tomato plants increase carotenoid concentrations as a defense mechanism against flooding stress.

Increasing flood duration affects electron flow and transport in photosystems

The OJIP fluorescence transient analysis provides detailed information on electron transfer processes in PSI and PSII, offering key insights into photochemical efficiency (Strasser et al. 2000). In particular, the maximum quantum efficiency of PSII (*F_v/F_m*) is widely used as an indicator of environmental stress tolerance (González et al. 2008). Our results showed that under 2-day flooding conditions, plant growth and water status decreased slightly, yet the *F_v/F_m* ratio remained stable (~0.8) (Fig. 4A). This suggests that tree tomato plants can sustain high PSII efficiency under short-term flooding, potentially due to the shading effect.

Tree tomato plants in the unshaded control treatment (CK) exhibited a slight reduction in photosynthetic performance compared to shaded control plants (0 d) (Fig. 4), aligning with findings from Zheng et al. (2024) for this species. This supports the idea that shading can slightly enhance photosynthesis in tree tomatoes grown in high Andean tropical regions. According to Ramírez-Soler (2021), tree tomato plants in these environments have a low light compensation point, meaning that excessive radiation may induce photoinhibition of the photosynthetic apparatus. Therefore, shading could play a role in modulating the species' response to flooding stress by reducing photoinhibition, which may help maintain efficient electron transport under stress conditions. Similarly, in lulo trees, the interaction between shading and flooding stress has been shown to partially mitigate oxidative damage to photosystems, preserving high *F_v/F_m* values (Sánchez-Reinoso et al. 2019). This suggests that the protective role of shading could be relevant for other Andean fruit species subjected to waterlogging stress.

The reduction in *F_v/F_m*, *PI_{ABS}*, *Φ_{PSII}*, and LEF indicated photochemical inhibition for the 4- and 6-day flooding treatments, which limited photosynthetic electron transport (Fig. 4A–D). This effect was also evident in *Solanum quitoense* plants under flooding (Sánchez-Reinoso et al. 2019). Decoupling the light phase from CO₂ fixation due to stomatal closure during flooding (Fig. 2A) causes a slowdown in electron movement within the photochemical machinery

(Zeng et al. 2021). The OJIP induction curves showed an increase in amplitude with the number of flooding days, reflecting a decrease in electron transport at the PSII donor site and at the final acceptors, such as quinone A (QA), quinone B (QB), and reduced plastoquinones (PQ^-) (Baba et al. 2016). Between steps O and J, the photochemical phase involved in quinone reduction (QA^-) is represented (Force et al. 2003). A higher peak in phase J and the increase in variable fluorescence at step J (V_J) in flooded plants (Fig. 5A, C) indicate a limitation in electron transfer at QA^- .

This phenomenon was confirmed by the values of ΨE_0 and ΦE_0 , which showed low probability and efficiency in transferring electrons from the trapped PSII (QA^-) to QB (Zivcak et al. 2014). The same effect was evident in step I, where the variable fluorescence (V_I) showed limitations in the transfer of electrons between QB^- and PQ (Fig. 5B–D). Additionally, in the 6-day flooding treatment during the recovery period, a K phase was observed during the induction curve (Fig. 5C), indicating inhibition of electron donation from the oxygen-releasing complex and changes in the architecture of the PSII antenna (González et al. 2008), which suggests a complete limitation in electron transport.

The increase in ABS, TR_0 , and DI_0 in flooded plants (Table 3) indicated a lower number of open (oxidized) reaction centers (RC) to receive an electron and a lower light absorption capacity (Toro-Tobón et al. 2022) compared to non-flooded plants. Furthermore, the limitation in electron transport (ET_0) and reduction of final acceptors of PSI (RE_0) were confirmed by the low values obtained in ΦRo and δRo , indicating a low yield and probability for an electron to effectively reach the final acceptors on the acceptor side of PSI, such as ferredoxin and $NADP^+$ (Force et al. 2003). Consequently, flooded plants showed increased values of Φ_{NO} and Φ_{NPQ} (Fig. 4E, F), indicating that they dissipate excess absorbed light energy as heat, avoiding the accumulation of reactive intermediates such as ROS (Tietz et al. 2017).

This supports the protection mechanism that tree tomato plants employ by increasing carotenoid concentrations (Table 2) and dissipating energy (DI_0). These data indicate that increased flooding duration reduces electron transport in PSII and PSI, making flooded tree tomato plants more susceptible to photoinhibition.

Increasing flood days decreased growth

With decreased water absorption, stomatal closure, and limitations in electron transport within the photosynthetic machinery, flooded tree tomato plants exhibited reduced biomass accumulation in both the root and aerial parts (Table 4). Studies on tomato, lulo, and eggplant under flooding conditions have similarly reported reductions in plant growth (Cardona et al. 2016). The S:R ratio revealed that root development decreased significantly compared to the

aerial parts of the plant. It is well established that the root is the primary organ affected by flooding, as it induces low oxygen levels in root cells, inhibiting aerobic respiration in the Krebs cycle and triggering the anaerobic pathway to temporarily maintain ATP levels (Zhang et al. 2019). However, this pathway generates toxic metabolites such as lactic acid, ethanol, and aldehydes, which lead to cell death and senescence (Pan et al. 2021). Additionally, cellular acidification (caused by lactic acid) leads to excessive generation of ROS, which increases during soil and root re-oxygenation (Jethva et al. 2022).

Interestingly, even in the absence of flooding, tree tomato plants grown without shade (CK) exhibited a lower leaf area compared to shaded, non-flooded plants (0 d). A similar effect was reported by Li et al. (2023) in tree tomato cultivated under moderate shade. This suggests that shading may contribute to greater leaf expansion, possibly as a response to lower light availability, allowing the plant to maximize light capture.

The significant reduction in leaf area and dry leaf mass with increasing flooding intensity can be attributed to leaf abscission, driven by elevated ethylene accumulation. As mentioned above, ethylene biosynthesis is enhanced as ACC, its precursor, is transported from the roots to the aerial parts, where it is converted into ethylene due to increased oxygen availability (Chen et al. 2024). This gaseous hormone plays a crucial role in regulating leaf senescence and abscission by inducing the expression of cell wall-modifying enzymes, such as cellulases and polygalacturonases, which weaken cell walls in the abscission zone (Chen et al. 2024). Consequently, plants experiencing prolonged flooding shed leaves as a survival strategy to reduce transpiration demand and conserve energy under stress conditions.

Conclusions

After 2 days of flooding, tree tomato plants showed slight reductions in g_s , Ψ_{leaf} , leaf angle, chlorophyll concentration, root growth (50%), and shoot growth (~25%), which could be considered mild stress. After 4 days of flooding, leaf pigments, plant water status, electron transport in PSII, and growth in leaves (68%), stems, and roots (71%) decreased significantly, classifying this as severe stress. Beyond this point, after 6 days of flooding, the physiological responses of the plants deteriorated further until reaching cell death. The plants did not survive the recovery period, with 100% leaf dehydration observed (Figs. 2–3), and reductions in leaf and root growth reached 80%.

It is important to highlight that all flooding treatments caused greater damage during the soil re-oxygenation phase and recovery period. Finally, a flooding duration of 4 days or more is considered a critical stress period

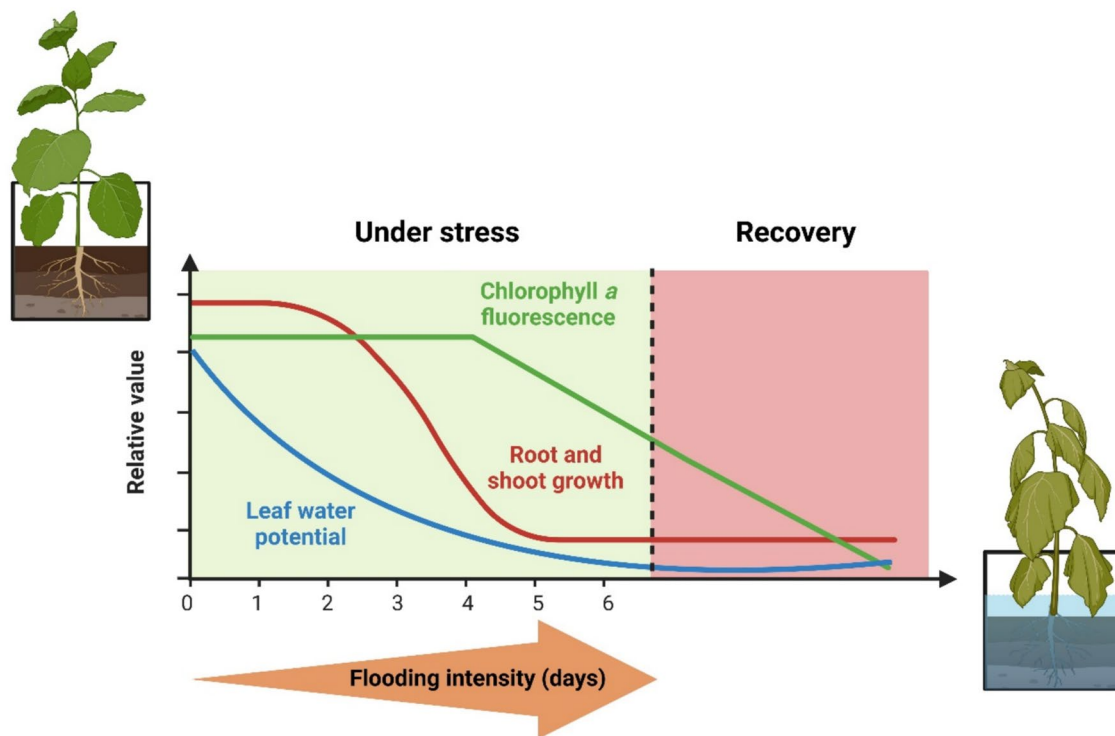


Fig. 6 Physiological model of flooding intensity on tree tomato physiological responses. The dotted line indicates the end of stress and the beginning of the recovery period. Created in BioRender

for tree tomato plants. This information is vital for fruit tree producers, enabling them to implement appropriate agronomic management strategies during flooding events (Fig. 6).

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Author contributions DAG-V: conception of the idea, taking measurements, data extraction and curation; formal analysis; investigation; methodology; software; visualization and original writing. HEB-L: formal analysis; methodology; supervision; writing—review and editing. OHA-S: formal analysis; methodology; writing—review and editing. J.G.A.-H.: formal analysis; methodology; writing—review and editing. L.M.M: formal analysis; methodology; writing—review and editing.

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Data availability Data are available through the corresponding author.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

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