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Physiological responses in commercial plants of the genus *Solanum* to flooding stress: a systematic review

Respuestas fisiológicas en plantas comerciales del género *Solanum* al estrés por inundación: una revisión sistemática

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***Solanum betaceum* plant with flooding symptoms.**
Photo: D.A. Gutiérrez-Villamil

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ABSTRACT

Flood events present a significant threat to global agricultural production, with an increasing likelihood of occurrence in the coming years due to climate variability. Commercial species of the genus *Solanum* are an integral part of the global food economy, due to their nutritional properties. However, their growth is threatened by flooding. The objective of this review was to analyze the current research status of the physiological response to flooding stress in *S. lycopersicum*, *S. tuberosum, S. melongena, S. quitoense, S. muricatum* and *S. betaceum*. A systematic review was conducted in accordance with PRISMA guidelines using four databases. A total of 1,364 relative change data points were obtained from 41 scientific articles to evaluate the behaviour of variables related to water status, photosynthesis and growth under flooded versus non-flooded conditions. The tomato was the most studied species under flood stress, in contrast to the potato, tree tomato, and sweet cucumber. In conclusion, the results demonstrated that flood stress reduced water status, photosynthesis and growth in commercial *Solanum* plants by 32, 25 and 29%, respectively. These findings indicate that these species are highly vulnerable to waterlogging. This review identifies research gaps in the physiology of crops belonging to the genus *Solanum* that should be addressed in future studies to contribute to plant tolerance to flood stress.

Addicional key words: Solanaceae; gas exchange; chlorophyll; hypoxia; morphological traits.

RESUMEN

Los eventos de inundación amenazan la producción agrícola mundial, y se espera que su ocurrencia aumente en los próximos años debido a la variabilidad climática. Las especies comerciales del género *Solanum* hacen parte de la economía mundial alimentaria gracias a sus propiedades nutricionales. Sin embargo, el crecimiento de estas plantas se ve amenazado por el anegamiento. El objetivo de esta revisión fue analizar el estado actual investigativo de la respuesta fisiológica al estrés por anegamiento en las especies *S. lycopersicum, S. tuberosum, S. melongena, S. quitoense, S. muricatum* y *S. betaceum*. Se realizó una revisión sistemática de acuerdo con las directrices PRISMA utilizando cuatro bases de datos, donde se obtuvieron 1.364 datos de cambio relativo de 41 artículos científicos para evaluar el comportamiento de las variables relacionadas con el estado hídrico, fotosíntesis y crecimiento en condiciones de inundación en comparación con las no inundadas. La especie más estudiada en el estrés por inundación fue el tomate, a diferencia de la papa, tomate de árbol, y pepino dulce. En general, el estrés por inundación redujo 32, 25 y 29% el estado hídrico, la fotosíntesis y el crecimiento en las plantas comerciales de *Solanum*, respectivamente, lo que hace estas especies muy vulnerables al anegamiento. En esta revisión, se identificaron vacíos en la investigación de la fisiología de cultivos pertenecientes al género *Solanum* que deberían abordarse en futuros estudios para contribuir a la tolerancia de las plantas al estrés por inundación.

Palabras clave adicionales: Solanaceae; intercambio gaseoso; clorofila; hipoxia; rasgos morfológicos.

INTRODUCTION

The Solanaceae family is the third most economically important plant family, encompassing species vital to agriculture, medicine, and human nutrition (Ghatak *et al*., 2017). *Solanum*, the largest genus in this family, includes over 2,000 species and has been the focus of extensive chemical and biological research in recent decades (Delbrouck *et al*., 2023; Borsoi *et al*., 2024). Key food crops such as *Solanum tuberosum* (potato), *S. lycopersicum* (tomato), *S. melongena* (eggplant), and *S. muricatum* (sweet cucumber) belong to this genus. Additionally, Andean-native fruits like *S. betaceum* (tree tomato) and *S. quitoense* (lulo) are of growing importance. These fruits are rich in phytochemical flavonoids, phenolic acids, alkaloids, and saponins—that support human health and help reduce disease risk (Elizalde-Romero *et al*., 2021).

In recent years, crop yield and quality worldwide have been affected by the variability of hydrometeorological events caused by climate change, such as increased rainfall and flooding (Ortiz-Bobea *et al*., 2021). In this context, Liu *et al*. (2023) projects that the frequency of flooding and waterlogging stress in crops may increase by 20% over the next 57 years due to global warming, highlighting the need to study plant responses and adaptations to flooding.

Flooding affects global agricultural production by prolonged soil waterlogging, which disrupts optimal plant development. Soil waterlogging occurs when plant roots are exposed to excessive water, reducing the availability of oxygen (O_2) in the soil (radical hypoxia) and impairing root respiratory metabolism (Sasidharan *et al*., 2017). These conditions induce physiological stress that negatively affects plant photosynthesis, growth, development, and crop yield. The severity of these effects depends on crop type, growth stage, and stress intensity (Jia *et al*., 2021; Tian *et al*., 2021; Fischer *et al*., 2023). Many commercially important *Solanaceae* species are susceptible to waterlogging stress and exhibit distinct physiological response mechanisms (Hartman *et al*., 2020; Fischer *et al*., 2021). To respect, Niu *et al*. (2023) reported that waterlogging reduced stomatal conductance, net photosynthesis, and transpiration rate.

Considering the global commercial importance of *Solanum* species and the increasing frequency of flooding events due to climate change, this review aims to present the current research status on the physiological responses and mechanisms to flooding stress in *S. lycopersicum, S. tuberosum, S. melongena, S. quitoense, S. muricatum,* and *S. betaceum*. Specifically, it seeks to address the following questions: Which agronomically important *Solanum* species have been studied under flooding conditions? What methodological approaches have been used to simulate flooding? How does root flooding affect photosynthesis, water status, and growth in these species?

METHODOLOGY

Design and planning

Scientific information was gathered from four databases (Scopus, Web of Science, SciELO, AGRIS) covering the period from 1995 to November 2024 to collect as much relevant data as possible on flooding in *Solanaceae* species over the past 30 years. The following keywords were used: “Solanum lycopersicum”, “Solanum tuberosum”, “Solanum melongena”, “Solanum quitoense”, “Solanum betaceum”, “Solanum muricatum”, “waterlogging”, “flooding”, “hypoxia”, and “waterlogged” as well as other common names for these species, translated into Spanish, English, and Portuguese. The species *Ipomoea batatas* (sweet potato) was excluded due to its similarity with the common name of potato. Using these keywords, search queries were constructed for each database, resulting in a total of 1,184 scientific documents (Scopus: 567; Web of Science: 604; AGRIS: 1; SciELO: 12).

The selection and eligibility process was conducted based on the following inclusion criteria: (1) only original scientific articles, (2) studies involving controlled flooding stress in the selected *Solanum* species, (3) experimental designs that included flooded vs. non-flooded treatments, and (4) studies that quantified variables directly related to photosynthesis, water status, and growth parameters (at least one of these). After applying the criteria, a total of 41 scientific articles were selected for the review.

Data extraction

The variables selected for data extraction were divided into three categories. First, plant water status: stomatal conductance (g_s), transpiration (*E*), leaf water potential (Ψ_L), root hydraulic conductivity (Lpr), leaf or petiole angle, and intrinsic water use efficiency (WUE_i). Second, photosynthetic performance variables, including relative chlorophyll content (SPAD), chlorophyll concentration, RuBisCO activity, maximum quantum efficiency of PSII (Fv/Fm), effective quantum yield of PSII (ΦPSII), photochemical quenching (qP), non-photochemical quenching (NPQ), relative electron transport rate (ETR), CO_2 assimilation rate, and internal CO_2 concentration. Third, variables related to growth and morphological traits, such as root length (RL), root area (RA), root volume (RV), root dry mass (RDW), shoot dry mass (SDW), total dry mass (TDW), shoot-root ratio (S:R), stem diameter, leaf thickness, and leaf area.

For each selected article, the absolute values of the response variables (from tables or figures) were recorded in an Excel file using the WebPlotDigitizer 4.7 program (https://apps.automeris.io/wpd/), following the methodology outlined by Burda *et al*. (2017). The relative change (increase or decrease) in each variable under flooding treatment, compared to the control treatments (well-watered plants), was calculated using Equation 1, which corresponds to an observation. Observations were calculated independently of the factors being evaluated (e.g., genotypes, stress intensity, priming), if the comparison was between flooded and non-flooded treatments. For variables measured over time, observations were taken at each sampling point.

$$Relative change = \frac{(Treatment value - Control value)}{Control value} \tag{1}$$

In addition, information was extracted from the methodology of each analyzed article, such as the number of observations in the crop species, flooding methodology, environmental conditions of the experiment (greenhouse, open field, or growth chamber), culture medium (pots or soil), and the implementation of controlled shading. Relative change data were graphed using the ggplot2 library version 3.4.2 (Wickham, 2016) of the R software version 4.3.0.

RESULTS AND DISCUSSION

Methodological approaches in flood stress

Of the articles investigating physiological responses to flooding stress in *Solanum* crops, 78% focus on the cultivation of tomato, followed by tomato and eggplant (Tab. 1). One study reported the analysis of flooding in tomato genotypes grafted onto eggplant, and since physiological responses may vary with graft interactions, this was considered as a separate species. Additionally, potato, tree tomato, and sweet cucumber are the species with the fewest studies conducted (Tab. 1), and no research has been reported on the influence of flooding on physiological responses in sweet cucumber.

Table 1. Methodological approaches of the articles analyzed.

Approach		Relative frequency (%)
Studies in *Solanum* crops	Tomato	78.05
	Potato	2.44
	Eggplant	7.32
	Tomato×Eggplant	2.44
	Lulo	7.32
	Tree tomato	2.44
	Sweet cucumber	0
	Total	100
Flood methodology	Sheet of water above the ground	92.68
	Partial flooding of the soil	2.44
	Oxygen levels in the nutrient solution	4.88
	Total	100

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Environmental conditions of the experiment	Greenhouse, planted in pots	60.98
	Greenhouse, grown in hydroponics	2.44
	Growth chambers, sowing in pots	31.71
	Open field conditions, soil	4.88
	Total	100
Shadow simulation	Yes	7.32
	No	92.68
	Total	100

The most common method to induce flooding or hypoxia stress was maintaining a water layer above the soil during the evaluation period (Tab. 1) (Bhatt *et al*., 2015; de Pedro *et al*., 2020; Geldhof *et al*., 2023). Only 4.88% of studies used dissolved O_2 concentrations in nutrient solutions to create hypoxic conditions (Nada *et al*., 2004; Mauro *et al*., 2020). Partial root flooding was explored in just one study using specialized root chambers (Dresbøll *et al*., 2013). Most experiments were conducted in greenhouses or growth chambers with pots, while only two studies were carried out in open field conditions (Sarker *et al*., 2023b; Yin *et al*., 2023). Additionally, 92.68% of the studies did not include artificial shading, despite its relevance for simulating low-radiation conditions typical of rainy seasons (Baracaldo *et al*., 2014; Cardona *et al*., 2016; Sánchez-Reinoso *et al*., 2019).

Tomato is the most studied *Solanum* species, likely due to its economic importance and role as a model dicot in plant biology (Liu *et al*., 2022). Over the past 30 years, significant progress has been made in understanding its response to flooding. In contrast, other agronomically important *Solanum* species remain understudied, including tree tomato (Betancourt-Osorio *et al*., 2016), lulo (Flórez-Velasco *et al*., 2015; Cardona *et al*., 2016; Sánchez-Reinoso *et al*., 2019), potato (Orsák *et al*., 2023), eggplant (Sarker *et al*., 2023a, b), and tomato×eggplant grafting (Bhatt *et al*., 2015). No studies were found for sweet cucumber. Expanding research in these species is crucial for identifying traits useful in breeding for stress tolerance (Jia *et al*., 2021).

Most flooding experiments in *Solanum* have been carried out under controlled conditions (greenhouses or growth chambers) using pots (Tab. 1). While such environments reduce experimental variability, they may not reflect real-world field conditions, which are more variable (Forero *et al*., 2019). Only two studies included in this review were conducted in open field settings: one on eggplant (Sarker *et al*., 2023a) and one on tomato (Yin *et al*., 2023). Future research should integrate both greenhouse and field approaches for a more comprehensive understanding.

Flooding is typically induced by maintaining a water layer above the soil. Tian *et al*. (2021) found a strong link between water depth and yield reduction, likely due to limited oxygen diffusion—reduced by up to 95% during flooding. Higher water levels worsen hypoxia in the root zone, leading to greater physiological stress.

Another key factor is shading. Excess rainfall often reduces light availability due to cloud cover (Ren *et al*., 2023). Some studies incorporated shading, such as in tomato (Baracaldo *et al*., 2014) and lulo (Cardona *et al*., 2016; Sánchez-Reinoso *et al*., 2019), indicating that shading improved plant tolerance to flooding.

Plant water relations under flood stress

In the variables related to plant water status under flooding stress in *Solanum* crops, 386 data points were obtained from 18 of the 41 articles analyzed. Of these, 10 data points were for Lpr, 136 for g_s, 68 for Ψ_L, 104 for *E*, 62 for leaf angle, and 6 for WUE_i (Fig. 1). The data revealed that Lpr and g_s decreased to a greater extent (an average of 45and 44%, respectively) due to flooding compared to the other variables (Fig. 1). In general, the variables related to plant water status (Lpr, g_s, E, Ψ_L) showed a median relative change of 35.74%. Leaf angle and WUE_i increased under flooding stress. These results suggest that some commercial *Solanum* species exhibit limitations in the absorption and movement of water from the roots to the atmosphere under flooding.

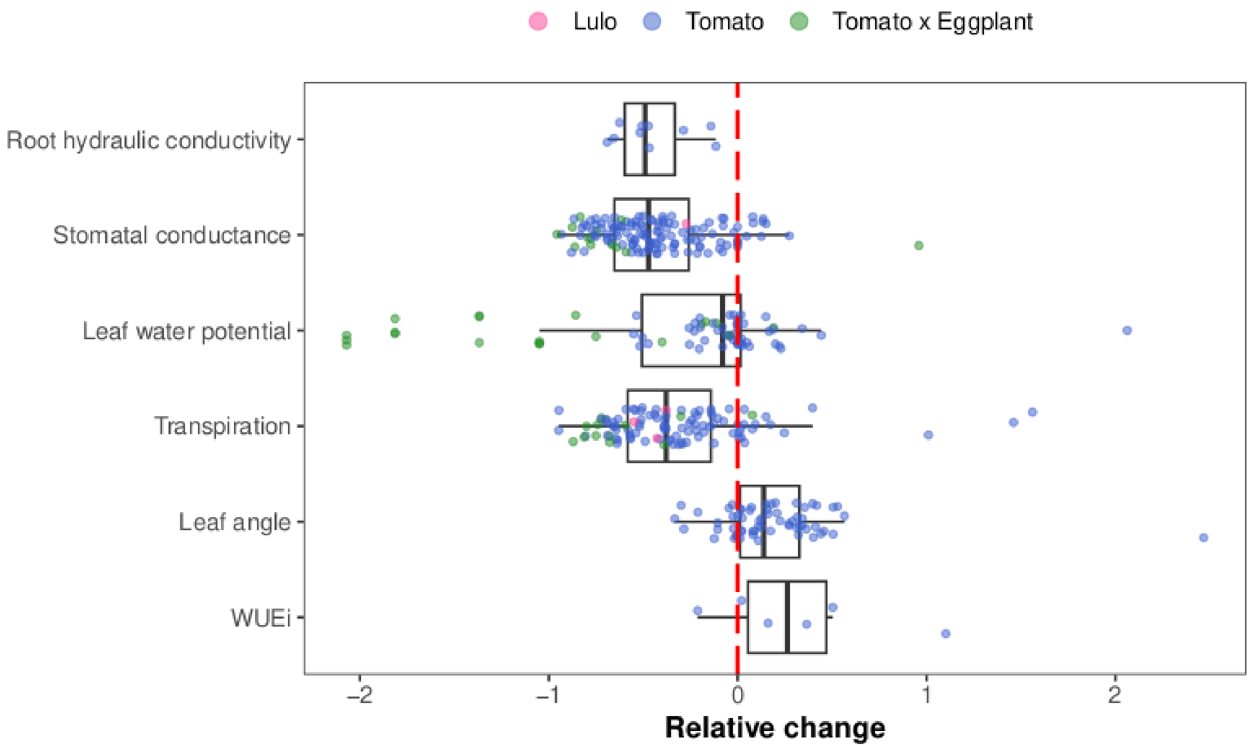

Figure 1. Relative change in variables associated with water status in commercial species of the *Solanum* genus under flooding. Each point within the boxplot represents the observation data of the flooded treatment compared to the control (*n*=386). The red dashed line indicates zero.

Regarding the crops, lulo, tomato, and tomato×eggplant were the only species that presented data on the water variables, leaving a gap in information for tree tomato, potato, and eggplant under flood stress (Fig. 1). It is important to mention that in tomato×eggplant, Ψ_L and g_s are more affected than in tomato. This may indicate a differential effect of these variables because of grafting. This is interesting, and we suggest studying it in more detail.

The Lpr and Ψ_L are key indicators of plant water status and typically decrease under flooding (Rodríguez-Gamir *et al*., 2019; Fig. 1). Water transport under hypoxia often relies on aquaporins (AQPs), which are activated as an adaptive response (Kudoyarova *et al*., 2022). Flooding can also cause xylem embolisms, reducing water transport efficiency (Martínez-Arias *et al*., 2022; Fig. 2). In tomato, Lpr remained stable during flooding, likely due to regulated expression of membrane aquaporins (PIPs) (Molina *et al*., 2014), supporting water balance under soil hypoxia (Jethva *et al*., 2022). However, this AQP-flooding interaction remains unstudied in other commercial *Solanum* species.

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Signaling from the root to the shoot of the plant is primarily regulated by changes in xylem pressure (Chaumont and Tyerman, 2014), which influences *E* and Lpr (Rodríguez-Gamir *et al*., 2019). In tomato plants, a reduction in g_s, Ψ_L, and *E* has been observed as an early response to waterlogging (<12 h) (Jackson *et al*., 2003). Furthermore, it has been shown that, during flooding stress, abscisic acid (ABA) and pH, apparently, do not act as chemical signals in the redistribution of water from the root xylem to the shoot (Else *et al*., 2006). However, there is a hydraulic signal that appears to be the primary mechanism informing the plant of stress. This hydraulic signal induces leaves ABA synthesis, which in turn signals stomatal closure in tomato leaves under waterlogging conditions (de Ollas *et al*., 2021).

In tomato plants under flooding, leaf angle increases due to the accumulation of ethylene and ABA in the petiole (Geldhof *et al*., 2023). Ethylene levels rise in the shoot because its precursor, 1-aminocycloproPane-1-carboxylic acid (ACC), is produced in hypoxic roots and transported via the transpiration stream to the leaves, where it is converted to ethylene in the presence of O_2 (Chen *et al*., 2024; Khoury *et al*., 2024) (Fig. 2). This mechanism is supported by the detection of high ACC concentrations in xylem sap after 24 h of flooding (Else and Jackson, 1998). While leaf angle is negatively correlated with g_s and Ψ_L due to epinastic movement during dehydration (Briglia *et al*., 2020), current data show a strong correlation between leaf angle, water status, and ethylene signaling under flooding conditions (Fig. 1). Therefore, leaf angle could serve as a practical indicator of waterlogging intensity and plant physiological response in commercial *Solanum* species.

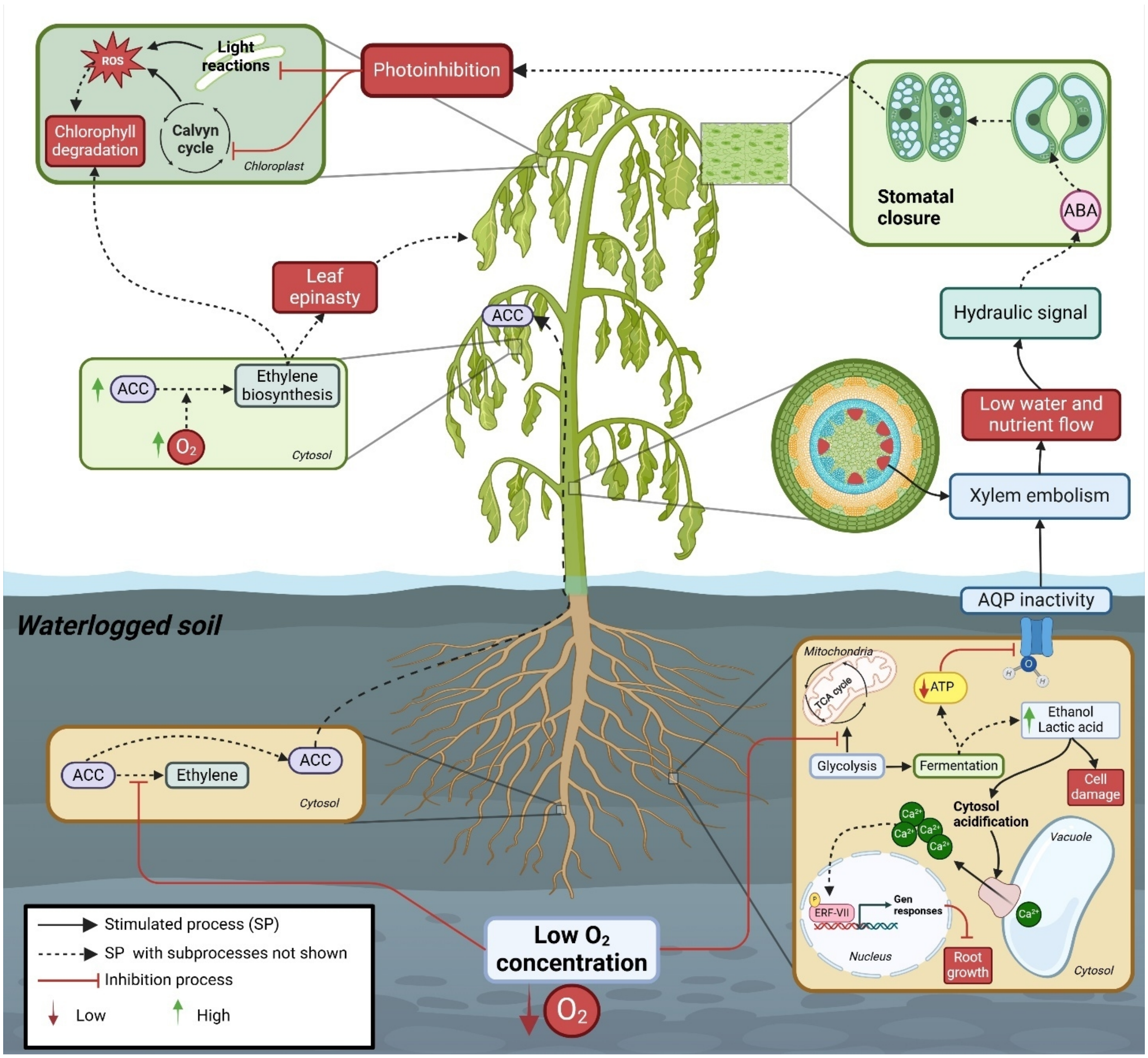

Figure 2. Molecular and physiological mechanisms involved in some responses of *Solanum* plants to waterlogging stress. ACC: 1-aminocyclopropane-1-carboxylate. AQP: aquaporins. TCA: tricarboxylic acid. ATP: adenosine triphosphate. ERF: ethylene response factor. ABA: abscisic acid. ROS: reactive oxygen species. Created in BioRender.

When flooding stress is combined with a reduction in light intensity (shading), leaf angle may be affected. Shading typically causes leaves to remain more horizontal, optimizing light capture for photosynthesis (Mullen *et al*., 2006), and this may delay the increase in leaf angle that usually occur because of dehydration caused by flooding. However, flooding could induce leaf epinasty more efficiently than other abiotic stresses due to the high concentration of ethylene it produces, which plays a key role in regulating this morphological trait, as previously discussed.

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Lulo, tomato, and tomato×eggplant plants exhibited variables related to the plant's water status. However, similar data were not found for potato and tree tomato crops, creating a knowledge gap regarding the physiological responses to waterlogging in these species. This species are susceptible to flooding stress, which reduces water uptake and movement within the plant. This reduction occurs through both physical mechanisms (Lpr) and possibly biochemical signals (such as ethylene and ABA).

Plant photosynthetic responses to flooding stress

With stomatal limitation and reduced water transport through the plant, gas exchange and CO_2 uptake are influenced by flooding conditions. The variables related to the photosynthetic process included 709 data points, which were extracted from 21 of the 41 articles analyzed. The SPAD variable had the highest number of observations, with 154 data points. In contrast, RuBisCO activity had only two observations (Fig. 3). In general, the photosynthetic performance variables decreased by 11.76% (median). Most of the parameters associated with photosynthesis showed a decrease due to flooding stress in all commercial *Solanum* species, especially CO_2 assimilation, (median of 40.65%). The total chlorophyll concentration showed a reduction of 19.3%, with chlorophyll *a* exhibiting a greater decrease (15.65%) compared to chlorophyll *b*. The variables associated with chlorophyll *a* fluorescence showed slight changes. However, NPQ showed a moderate increase (median of 29.41%) in response to the interruption of the photosynthetic process.

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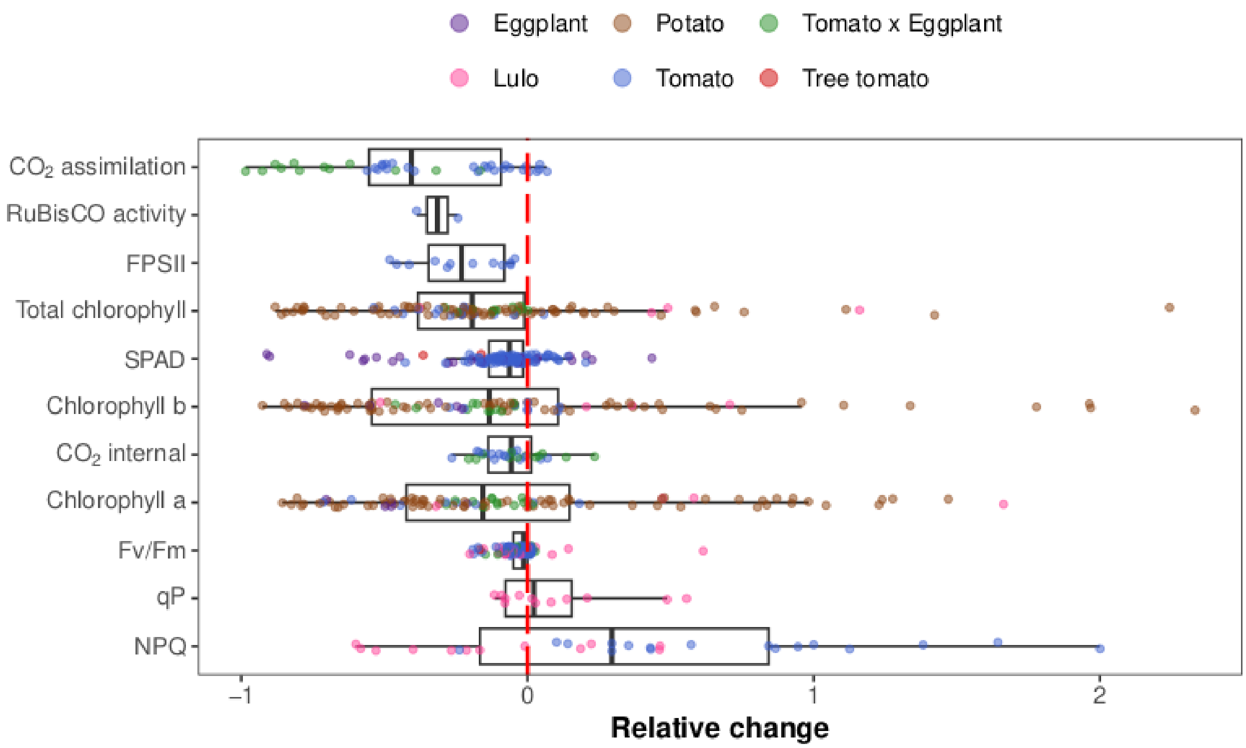

Figure 3. Relative change in variables associated with photosynthetic performance in commercial species of the *Solanum* genus under flooding. Each point within the boxplot represents the relative change of the flooded treatment compared to the control (*n*=709). The red dashed line indicates zero.

All species, except sweet cucumber, showed data for variables associated with photosynthesis, though not all species to the same extent. Tomato exhibited data for all photosynthetic variables (Fig. 3), with most values centred around zero, indicating minimal relative changes. Lulo and potato showed greater variability, particularly in chlorophyll-related parameters. Eggplant displayed a more consistent response with less dispersion. The tomato×eggplant hybrid showed a positive trend in CO_2 assimilation, suggesting improved photosynthetic efficiency. Tree tomato had data only for SPAD and Fv/Fm, with minimal relative changes. These results highlight species-specific responses in photosynthetic traits.

Photosynthetic responses in commercial *Solanum* species show a general decline in key parameters under waterlogging (Fig. 3), consistent with previous findings (Tian *et al*., 2021; Tahjib-Ul-Arif *et al*., 2023). This stress impairs root function, reduces water flow, and lowers g_s, limiting photosynthesis (Fig. 2). Reduced g_s slows the Calvin cycle and RuBisCO activity, leading to energy imbalance and increased ROS production, which can damage PSII and trigger protective dissipation mechanisms (Zhang *et al*., 2021). Although RuBisCO activity has been

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evaluated in flooded tomato plants (de Pedro *et al*., 2020), data for other *Solanum* species remain unavailable.

Limited energy use for CO_2 fixation under flooding activates alternative dissipation mechanisms, such as heat dissipation (NPQ), detectable via chlorophyll fluorescence (Flórez-Velasco *et al*., 2024) (Fig. 3). In tree tomato, reduced PSII efficiency (Fv/Fm) has been reported under prolonged stress (Betancourt-Osorio *et al*., 2016) (Tab. 1). Photoinhibition decreases chlorophyll content in several *Solanum* species (Flórez-Velasco *et al*., 2015; Orsák *et al*., 2023) (Fig. 3). Ethylene accumulation in shoots during flooding may also induce senescence and promote chlorophyll degradation (Khoury *et al*., 2024) (Fig. 2). Interestingly, in potato, flooding sometimes increases chlorophyll levels, potentially indicating tolerance (Orsák *et al*., 2023). Identifying waterlogging-tolerant genotypes is crucial to mitigate crop losses from future climate-driven flooding events (Liu *et al*., 2023).

However, not all species exhibited this behavior, and many lack comprehensive data on all variables. For instance, in tree tomato, only relative chlorophyll content (SPAD) and Fv/Fm were assessed (Fig. 3). The photosynthetic metabolism of the analyzed *Solanum* species is highly sensitive to waterlogging stress, as it inhibits light capture, energy transfer in photosynthetic pigments, and ETR, ultimately leading to a reduction in CO_2 assimilation.

Responses in plant morphological traits and growth to flood stress

269 observations were obtained from 20 of the 41 articles analyzed. In general, all variables showed a decrease in response to flood stress, with a relative change of 34.36%, except for root diameter and the S:R ratio, which increased by 10.1 and 40.68%, respectively (Fig. 4). It should be noted that RV was the most affected variable, decreasing by 63% compared to non-flooded treatments (Fig. 4). The variable with the most observations was leaf thickness (51), while RD had the fewest data points (2).

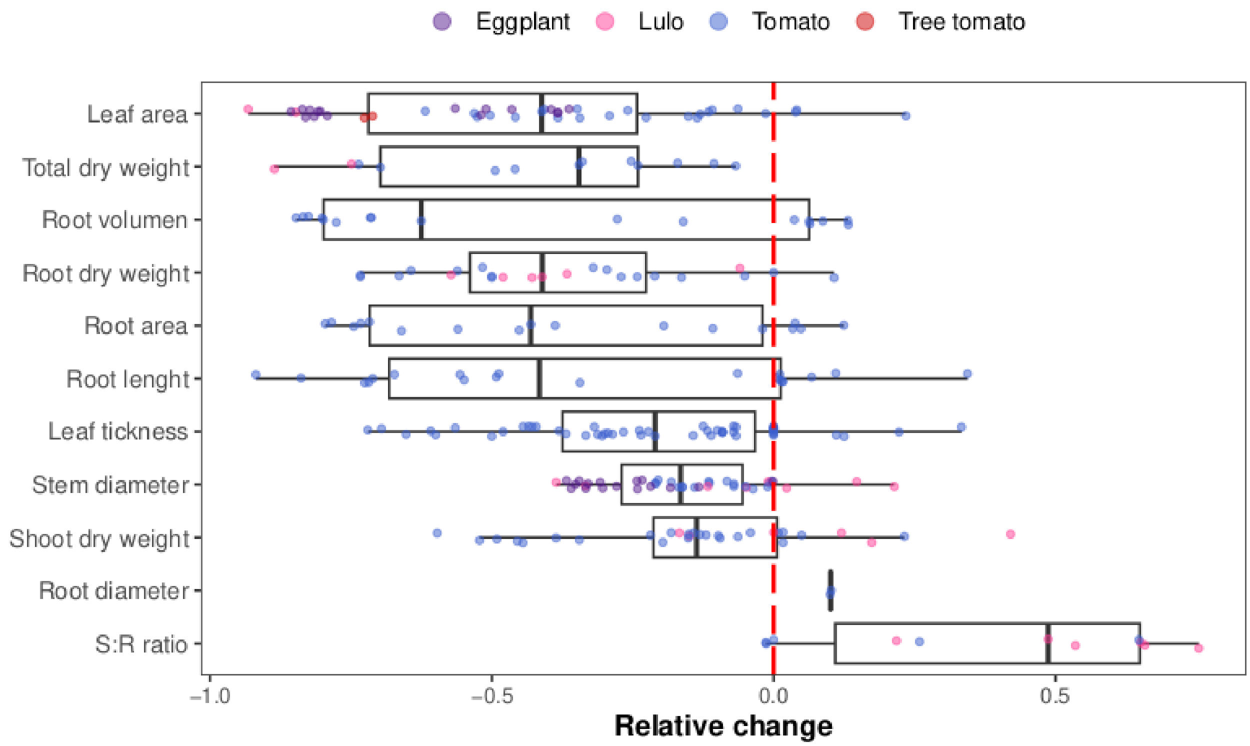

Figure 4. Relative change of variables associated with growth and morphological traits in commercial species of the genus *Solanum* under flooding. Each point within the boxplot represents the relative change of the flooded treatment compared to the control (*n*=269). The red dashed line indicates zero.

Waterlogging stress severely impacts root and shoot growth, with roots being most affected due to oxygen deficiency in the soil (Khoury *et al*., 2024). Under hypoxia, essential processes like the TCA cycle and oxidative phosphorylation are disrupted, reducing ATP production (Fischer *et al*., 2023). To compensate, plants shift to fermentative respiration, producing ATP via glycolysis, but also accumulating toxic byproducts such as lactate, ethanol, and acetaldehyde, which damage cells (Kagenishi *et al*., 2023) (Fig. 2). Lactate-induced cytosolic acidification activates vacuolar Ca^{2+}-ATPases, increasing cytosolic Ca^{2+} levels (Igamberdiev and Hill, 2018). This calcium signal triggers phosphorylation of ERF-VII transcription factor, repressing auxin-induced genes crucial for lateral root development (Shukla *et al*., 2019; Fan *et al*., 2023) (Fig. 2). Overall, waterlogging impairs root growth by limiting energy production and activating stress pathways that inhibit root system formation.

Functional root damage during soil flooding leads to limited absorption and transport of water and nutrients. Water transport from the root is affected by the inactivation of AQPs, due to ATP deficiency in the cell, as ATP is necessary for the phosphorylation of AQPs (Kudoyarova *et al*.,

2022) (Fig. 2). This may negatively impact the growth and development of the shoot. However, the relative increase in S:R ratio indicates a more drastic reduction in root biomass compared to the shoot biomass. Consequently, parameters such as SDW, SD, leaf thickness, and leaf area decrease considerably under flooding (Fig. 4). Despite the impacts on growth variables during flooding in some species, these parameters have not been reported for potato and eggplant. Therefore, it is pertinent to investigate the effects of flooding on the morphological responses of these solanaceous plants.

CONCLUSIONS AND FUTURE PERSPECTIVES

The water status, photosynthesis, and growth of commercial *Solanum* species are significantly impacted when subjected to flooding stress. Tomato plants are the most extensively studied species worldwide in terms of their response to flooding. However, there remains a notable gap in knowledge regarding the physiological response to this stress in species like tree tomato and potato. Moreover, there is no available data on the physiological responses of sweet cucumber under flooding conditions. It is crucial to encourage further research into these species to better understand their flooding stress responses.

The most used methodology for inducing controlled flooding involves managing the water table above the soil, which has been shown to be negatively correlated with physiological damage in plants. Although controlling soil oxygen levels can also be effective, it often entails high costs and may not accurately replicate natural flooding conditions. Therefore, the above-ground water table method is recommended for its simplicity in inducing stress, while soil oxygen levels should also be monitored using sensors to obtain a more comprehensive understanding of the impact.

Given the potential challenges posed by climate change, it is essential to focus on the overall effects of waterlogging on *Solanum* crop yields, considering the factors identified in this review, as well as investigating the development of genotypes or rootstocks tolerant to waterlogging to ensure sustainable agricultural productivity. Finally, we consider it important to investigate topics related to the identification of physiological markers that indicate waterlogging tolerance.

Declaration of conflict of interest: the authors declare that they have no conflict of interest.

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