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Review article

Physiological and hormonal responses underlying salinity tolerance in wild tomatoes: Insights for cultivated varieties

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ABSTRACT

Soil salinisation is one of the main abiotic stress factors threatening modern agriculture, with over 1.3 million hectares affected worldwide and causing a progressive loss of arable land. Tomatoes are among the most important horticultural crops globally, but its moderate salt tolerance restricts productivity in saline soils. Related wild species, such as *Solanum pimpinellifolium* L., which have evolved in high-salinity environments, represent a valuable resource for studying adaptive stress responses and improving cultivated tomatoes. This study compares the salt stress response of *S. lycopersicum* L. and *S. pimpinellifolium* L. to identify the processes underlying the higher tolerance in wild species. Plants were grown hydroponically in a closed-loop system using two nutrient solutions: one mimicking seawater irrigation (33 % seawater, EC = 21 dS m^{-1}), and a salt-free control (0 % seawater, EC = 3.22 dS m^{-1}). Phenological, morphological, physiological, biochemical, and hormonal traits were assessed. *Solanum pimpinellifolium* L. effectively modulates the production of osmolytes and photoprotective compounds, the translocation of toxic ions, and improves leaf function which, in synergy with a more integrated and temporally coordinated hormonal network that sustain better growth, yield, and fruit quality under saline conditions. These findings provide new insights into the physiological basis of salt tolerance in wild tomato, supporting its value as a genetic resource and suggesting that seawater-based irrigation may serve as a framework for studying sustainable water management strategies.

1. Introduction

The development of stress-tolerant crops is a key challenge for ensuring sustainable agricultural production in the face of a growing global population and an increasingly critical climate change scenario (Tian et al., 2021). Among abiotic stresses, salinity is one of the most pressing constraints, causing substantial yield losses across major crops worldwide (Zhang et al., 2022a). According to the latest FAO report (FAO, 2024), salt-affected soils severely restrict plant growth and are widespread, particularly in arid and coastal regions, covering more than 1.38 billion. Salinisation arises from both natural processes, such as climate change (Hassani et al., 2021) and sea-level rise, and human activities including poor irrigation management and water overuse (Stavi et al., 2021). While aridity and rising water demand intensify risks in developing countries (Gomiero, 2016), the Mediterranean basin is especially vulnerable, here seawater intrusion into aquifers wetting front topsoils threaten crop productivity (Ferreira et al., 2022; Ghirardelli et al., 2024). Together, climate change and water scarcity converge to intensify salinity-induced yield losses worldwide.

Salt stress impairs water uptake, cell elongation, leaf growth and photosynthesis, while also disrupting protein and metabolite synthesis, ultimately constraining plant development and reproduction (Roşca et al., 2023). Plants, as sessile organisms, have evolved diverse strategies to counteract salt-induced damage (Zhao et al., 2021), including osmotic adjustment, ion homeostasis, compartmentalisation or exclusion of toxic ions, activation of antioxidant defences, and adjustments in growth and reproductive development (Zörb et al., 2019). Salt tolerance thus emerges not from a single trait but from a coordinated, multi-level response integrating molecular, physiological and phenological processes (Soltabayeva et al., 2021). Increasing evidence highlights

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phytohormones, and their intricate cross-talk, as central regulators orchestrating the “survive or die” strategies that plants adopt under salinity stress (Singh et al., 2022; Trivellini et al., 2016; Hussain et al., 2024).

Tomato (*Solanum lycopersicum* L.) is an established model for studying salinity tolerance (Yang et al., 2019). Domestication and intensive breeding have substantially reduced genetic diversity, limiting the adaptive potential of modern cultivars (Schouten et al., 2019). This erosion of agrobiodiversity underscores the importance of exploring wild relatives as reservoirs of traits for abiotic stress tolerance (Pailles et al., 2020). Concurrently, the reuse of marginal-quality water, including diluted seawater, is attracting attention as a sustainable irrigation strategy, particularly under climate change scenarios where water scarcity demands more efficient use of freshwater resources (Javeed et al., 2021).

Halophytes and salt-tolerant crops have therefore gained attraction as models for saline agriculture (Nikalje et al., 2018). However, the genetic variation available within cultivated species may be insufficient to sustain yields under increasing salinity, reinforcing the value of wild tomatoes as genetic resources (Li et al., 2023a,2023b). *Solanum pimpinellifolium* L., the closest relative of cultivated tomato, originates from saline coastal habitats of South America and displays natural adaptation to salt stress (Razali et al., 2018). In contrast, *S. lycopersicum* L. is less tolerant, serving as a useful comparator. Together, these species represent opposite extremes of the tolerance spectrum, enabling the identification of adaptive mechanisms with potential for breeding programmes. Importantly, *S. pimpinellifolium* is fully cross-compatible with *S. lycopersicum*, allowing the transfer of adaptive traits directly accessible to breeding via interspecific crossing and backcrossing (Gramazio et al., 2020).

Although many studies have described single aspects of plant responses to salinity—whether morphological, physiological (Eynizadeh et al., 2023) or hormonal (Ghanem et al., 2008), integrated and temporally resolved analyses remain scarce. Rootstock studies have shown that *S. pimpinellifolium* alleles can enhance scion ion balance, ABA transport and water status under salinity (Asins et al., 2010). However, these grafting-based approaches do not address how the intact wild plant regulates its own long-term physiological and hormonal responses. This gap is particularly evident for wild tomato relatives, both individually and in direct comparison with cultivated varieties. To our knowledge, no previous work has provided a comprehensive, multi-faceted characterisation of hormonal regulation in *S. pimpinellifolium* under salt stress, despite transcriptomic data suggesting the involvement of hormonal pathways (Zhao et al., 2017). Here, we address this gap by presenting an integrated analysis of morphological, physiological and yield-related traits, coupled with temporal hormone profiling and cross-talk, defined here as changes in hormone balance and coordinated regulation among ABA, cytokinins and other hormones, to clarify how these processes interact during prolonged stress. We further assess the potential of diluted seawater as a sustainable irrigation practice in horticultural systems. Building on this framework, this study was designed to investigate the responses underlying the contrasting behaviour of wild and cultivated tomato to salinity, aiming to (i) determine whether the wild species *S. pimpinellifolium* maintains growth, reproduction, and leaf functioning under prolonged salinity through coordinated phenological, morphological, and physiological adjustments compared with cultivated *S. lycopersicum*; to (ii) assess whether its superior tolerance is associated with enhanced osmotic adjustment and ion homeostasis that preserve water balance and cellular integrity; and to (iii) explore whether long-term hormonal networks align with these adaptive traits. We hypothesised that long-term salt tolerance in *S. pimpinellifolium* depends on enhanced osmotic and ionic adjustment together with the coordinated modulation of ABA, cytokinins and other hormones, enabling the maintenance of photosynthetic and reproductive functions under stress.

2. Materials and methods

2.1. Plant material, experimental set up and growth conditions

Two tomato species were used in this study: *Solanum lycopersicum* L. cv. ‘Principe Borghese’, a commercial cultivar known for its salt sensitivity (Cialli et al., 2024), and five accessions of *Solanum pimpinellifolium* L. Seeds of *S. lycopersicum* L. were supplied by Gargini Sementi (Lucca, Italy), while *S. pimpinellifolium* L. seeds were obtained from the Genebank Information System of the IPK (GBIS/I, Gatersleben, Germany; https://gbis.ipk-gatersleben.de/gbis2i/faces/index.jsf). The experiment was carried out at the Department of Agriculture, Food and Environment (DAFE), University of Pisa, Italy (lat. 43°42’42"N, long. 10°24’52"E) in a 100 m^2 glasshouse 12.5 m long and 8.0 m wide in rockwool substrate with recirculating nutrient solution. A growing system similar to a commercial closed-loop rockwool culture, was used. The glasshouse was equipped with automated side and roof windows (with insect screens), it wasn’t heated or shaded and it was subdivided into two independent compartments, effectively constituting two separate experimental units. Samples were collected from both compartments to ensure replication and maintain the independence of the treatments. A total of 192 plants were used in this study (32 plant per species, i.e. 16 per treatment, grown in 2 cultivation units per treatment), were arranged in a randomised treatment-stratified design, with each treatment distributed across the two sectors of the greenhouse. Seeds were sown on 25th January 2024 in small rockwool cubes and transplanted into standard rockwool slabs (1 m in length) on 11th March 2024. Each slab hosted four single-stem plants and seven drippers, with slabs arranged in pairs and placed side by side to achieve a planting density of approximately 3.57 plants m^{-2}.

Irrigation was automatically scheduled and adjusted throughout the growing period to deliver approximately 2.0 mm per event (60 s per irrigation), with a drainage fraction consistently maintained between 0.50 and 0.60 to prevent significant variations in electrical conductivity (EC) between the root zone and the mixing tank (Carmassi et al., 2025).

Greenhouse climate was monitored continuously using the Evja® system (https://www.evja.eu/solutions, accessed on 30 June 2024). During the cultivation period (from 11 March to 21 June), the average air temperature was 19.4°C (minimum = 6.5°C; maximum = 36.1°C), and the average relative humidity was approximately 75.8 % (ranging from 28.9 % to 98.2 % RHmax). The mean daily global radiation (GR) measured inside the greenhouse was 8.88 MJ m^{-2}, with minimum and maximum values of 0.51 MJ m^{-2} and 16.07 MJ m^{-2}, respectively.

A single salt stress treatment was applied using a nutrient solution prepared with artificially diluted seawater (Salt), while the control solution was based on tap water and supplemented with macro- and micronutrients (Non Salt) to meet the nutritional requirements of *S. lycopersicum* and *S. pimpinellifolium.* The saline nutrient solution was prepared by mixing a recreated seawater, derived from a 10 × stock solution of synthetic sea salt (350 g L^{-1} Instant Ocean® dissolved in tap water), with the nutrient mix until the desired EC was reached. Salinity was applied gradually, beginning 15 days after transplanting, with daily EC increases of approximately 1.0 dS m^{-1} to minimise the risk of osmotic shock. The control solution (Non Salt) had an EC of 3.2 dS m^{-1} (approximately 30 mmol L^{-1}), while the salt treatment solution (Salt) reached an EC of 21 dS m^{-1}, corresponding to 35 % seawater (approximately 198 mmol L^{-1}). The molarity of the two nutrient solutions is calculated by taking the molarity of seawater, which is 600 mmol L^{-1}, as a reference and was then calculated as a percentage.

Nutrient solutions were prepared using either tap water (Non Salt NS) or synthetic seawater (Salt NS) and supplemented with analytical-grade salts (Carlo Erba Reagents, Milano, Italy), considering the ionic contribution of the tap or seawater used in the preparation as follows:

- Non Salt NS (EC = 3.22 dS m^{-1}): 13.06 mmol L-1 ol L^{-1} N–NO_3^-; 1.00 mmol L^{-1} N–NH_4^+; 1.20 mmol L^{-1} P; 12.00 mmol L^{-1} K;

6.00 mmol L^{-1} Ca; 3.00 mmol L^{-1} Mg; 0.86 mmol L^{-1} Na; 6.91 mmol L^{-1} S–SO_4^{2-}; 15.00 µmol L^{-1} Fe; 20.0 µmol L^{-1} B; 1.0 µmol L^{-1} Cu; 5.2 µmol L^{-1} Zn; 10.0 µmol L^{-1} Mn; 1.0 µmol L^{-1} Mo.

- Salt NS (EC = 19.88 dS m^{-1}): 13.00 mmol L^{-1} N–NO_3^-; 1.0 mmol L^{-1} N–NH_4^+; 1.2 mmol L^{-1} P; 14.72 mmol L^{-1} K; 6.00 mmol L^{-1} Ca; 16.00 mmol L^{-1} Mg; 147.50 mmol L^{-1} Na; 11.07 mmol L^{-1} S–SO_4^{2-}; 192.80 mmol L^{-1} Cl^-; 15.0 µmol L^{-1} Fe; 137.1 µmol L^{-1} B; 1.0 µmol L^{-1} Cu; 6.3 µmol L^{-1} Zn; 10.0 µmol L^{-1} Mn; 1.0 µmol L^{-1} Mo.

The pH of the recirculating nutrient solution was regularly checked and adjusted to remain within the range of 5.50–6.50, using sulphuric acid when necessary. The nutrient solution was replaced when EC exceeded 4.7 mS cm^{-1} in the Non Salt NS and 22.5 mS cm^{-1} in the Salt NS.

The salinity treatment lasted for a total of 83 days, with destructive sampling conducted every 21 days. Table 1 summarises the experimental timeline, including the setup and sampling dates, as well as the number of days elapsed since the onset of salinisation for each sampling point.

The five *S. pimpinellifolium* accessions (WR2, LYC2824; WR9, LYC2794; WR10, LYC2750; WR11, LYC2665; WR14, LYC2914) and the commercial variety of *S. lycopersicum* ('Principe Borghese') used in this study —were originally selected from previous *in vitro* screening studies for salinity tolerance (Cialli et al., 2024, 2025). All five wild accessions, along with 'Principe Borghese', were cultivated under identical greenhouse conditions and exposed to 35 % seawater salinity stress throughout the entire experiment. At the final sampling point, a comparative morphological assessment was performed among the *S. pimpinellifolium* accessions, including measurements of plant height, dry biomass weight, number of nodes, and number of leaves. This screening aimed to identify the most salt-tolerant wild genotype under realistic greenhouse conditions and to select it for subsequent detailed physiological and hormonal analysis.

2.2. Phenological and morphological measurements

Phenological and morphological traits were assessed throughout the cultivation period under Non Salt and Salt stress conditions. Phenological evaluation focused on inflorescence development and was performed weekly on six plants per accession/cultivar per treatment. The number of inflorescences along the main shoot was recorded according to the BBCH Monograph (Cardoso et al., 2021; Growth Stage 6: Flowering, BBCH code 61). Morphological measurements were carried out destructively at each sampling on three biological replicates per accession/cultivar per treatment. Fresh weight (FW, g) was recorded, and dry weight (DW, g) was determined after oven-drying at 70 °C to constant weight, and dry residue (DR, %) was calculated as (DW/FW) × 100. Plant height (cm) was also recorded at each sampling.

2.3. Pigment content in leaves and fruits

For the extraction of leaves – carried out at time point T4 – and fruits – carried out at time point T3 –, two different matrices were used. Specifically, 500 mg of tissue from three fully expanded leaves frozen in liquid nitrogen and stored at –80 °C were used, while for fruits, 50 mg of freeze-dried fruit powder were used, following a modified protocol from Maggini et al. (2018). Samples were extracted one day before analysis with 5 mL methanol, using mortar and pestle under dim light conditions. After 30 min in cold ultrasonic bath and overnight storage at −20°C, the extracts were further sonicated for 30 min and filtered with Chromafil® Xtra PET-45/25 syringe filters (Macherey–Nagel, Duren, Germany) prior to HPLC analyses. The HPLC equipment (Jasco, Tokyo, Japan) consisted of a PU-2089 four-solvent low-pressure gradient pump and a MD-4010 diode array detector. The separation was performed with a C18 250/4.6 Nucleodur® 100–5 Isis column (Macherey–Nagel, Duren, Germany), using methanol (solvent A), acetonitrile (solvent B) and ethyl acetate (solvent C) as the eluents (Romeo et al., 2014). The elution program was set as follows: 25 %A-75 %B for 6 min, followed by 1.5 min linear gradient to 70 %A-30 %C, 3 min isocratic elution, 1.5 min linear gradient to the initial conditions and 8 min re-equilibration. The detection wavelength range was 270–700 nm and the chromatograms were recorded at 445 nm, with 1 mL min^{-1} flow and 20 µl injection volume. External calibration curves were obtained using standard solutions of the individual pigments, in appropriate concentrations according to the composition of the samples (Romeo et al., 2014). Pigment identification was based on retention times and UV–visible spectra compared to authentic standards. The analysed pigments included chlorophyll a, chlorophyll *b*, lutein, and violaxanthin for leaves and β-carotene and lycopene for fruits.

Table 1
Timeline of the salinity experiment, showing the dates and timing of sampling events relative to the onset of salinisation. T1 to T4 correspond to the first, second, third, and final sampling, respectively.

Sampling	Days after Transplanting	Days after Salinisation
T1	35	20
T2	56	41
T3	77	62
T4	98	83

2.4. Fruit quality and production analyses

Quality and production analyses were conducted on fruits at a uniform ripening stage, selected using a portable colourimeter (Minolta Camera Co. Ltd., Osaka, Japan). Fruit sampling was carried out at time point T3, corresponding to 62 days after the onset of salinisation. Organoleptic quality parameters were assessed, including the fresh weight of ten fruits (g) and pulp firmness (kg/cm^2). Fruit firmness was measured on five fruits per accession/cultivar per treatment using a digital penetrometer (mod. 53205 TR, Turoni & Co., Forlì, Italy) fitted with an 8 mm diameter tip. The maximum force (kg) required to penetrate the pulp was recorded (Cela et al., 2024).

After firmness analysis, the same fruits were cut into pieces and homogenised. A part of the puree was dried in an oven to obtain the dry matter content (DMC %). This was achieved by placing almost 25 g of fresh tomato puree in a laboratory oven (Memmert GmbH + Co. KG Universal Oven UN30, Schwabach, Germany) at 70 °C until a constant weight was reached. Another portion of puree was centrifuged at 1500 RCF for 15 min to extract the supernatant for chemical characterisation (Cela et al., 2024).

Total soluble solids (TSSs) were assessed using a refractometer (model ABBEREF 1, PCE Instruments, Meschede, Germany) and expressed as °Brix. Titratable acidity (TA) was determined by titrating against 0.1 M NaOH solution using phenolphthalein as an indicator and expressed as grams of citric acid per 100 g-1 fresh weight (FW) (Cela et al., 2024).

β carotene and lycopene, two major carotenoids in fruits, were also quantified to assess nutritional quality as described in paragraph 2.3.

2.5. Mineral analysis

Fully expanded leaves and roots sampled at the end of the experiment were dried at 70°C until constant weight. Then, a representative sub-sample of each tissue were ground using a laboratory mill. For the determination of mineral contents, a microwave-assisted acid digestion was performed following the protocol described by Fidalgo-Illesca et al. (2025). For each sample, 0.3 g of dry material was accurately weighed and digested with 8.0 mL of 65 % nitric acid in 70 mL Teflon vessels using the COOLPEX Smart Microwave Reaction System (Yiyao Instrument Technology Development Co., Ltd., Shanghai, China). After digestion, solutions were cooled to room temperature and diluted to a final volume of 30 mL with deionised water.

Potassium (K^+), sodium (Na^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) were quantified by atomic absorption spectrometry (Varian Model Spectra AA240 FS, Melbourne, Australia) as described by Carmassi et al. (2025). The analyses were performed in triplicate, and the results are expressed in g Kg^{-1}dry weight sample The accuracy of the measurements was tested using a tomato leaf, Certified Reference Material® 1573a (CRM 1573a), from the National Institute of Standards and Technology (Gaithersburg, MD, USA).

Selective transport (ST) of ion (K^+, Mg^{2+}, and Ca^{2+}) over Na^+ from root to leaf was estimated as follows (Hussain et al., 2023):

$$ST = \frac{ion/(ion + \quad Na^+)_{Leaf}}{ion/(ion + \quad Na^+)_{Root}}$$

2.6. Membrane leakiness

To assess membrane integrity, twenty leaf discs (1 cm^2 each) per replicate were excised from three fully expanded leaves. The discs were first rinsed in distilled water for 10 min to eliminate surface-bound electrolytes and those released from injured cells. After gently blotting dry, the discs were transferred into 25 mL of distilled water in Petri dishes and shaken at ambient temperature for four hours. Electrical conductivity (EC) of the bathing solution was then recorded (M1) using a conductivity meter (Basic 30, Crison, Barcelona, Spain). The same leaf discs were subsequently frozen at −20 °C overnight to ensure complete cell death. After thawing, a second EC reading (M2) was taken. Membrane permeability was calculated through electrolyte leakage, as the percentage ratio (M1/M2) × 100, representing the extent of ion leakage (Nali et al., 2004).

2.7. Osmolytes concentration

Leaf discs (1 cm^2 each), excised from three fully expanded leaves, were homogenised in distilled water at a ratio of 1 disc per 3 mL of water. The resulting homogenate was stored overnight at −20 °C to ensure complete extraction, then thawed and centrifuged at 1200 RCF for 15 min at room temperature. The osmolarity of the resulting supernatant was measured using an automatic freezing point osmometer (Osmomat 030, Gonotec, Berlin, Germany), previously calibrated with standard 300 mM sodium chloride solutions (Franzoni et al., 2021).

2.8. Relative water content

Relative water content (RWC%) was determined from three 1 cm^2 leaf discs per replicate, sampled from interveinal areas of three fully expanded leaves. RWC was calculated using the formula: [(FW − DW) / (SW − DW)] × 100, where FW is fresh weight, SW is saturated weight, and DW is dry weight. Saturated weight was measured after rehydrating the discs overnight on water-saturated filter paper in Petri dishes, while dry weight was obtained after oven-drying the samples at 80 °C for 24 h (Meucci et al., 2024).

2.9. Stomatal conductance

Stomatal conductance was measured using a portable porometer (AP4, Delta-T Devices Ltd., Cambridge, UK). The measurements were taken between 8.00 a.m. and 11.00 a.m.; in each treatment, 2 leaves were sampled from 3 to 6 individual plants, sampling three fully expanded leaves (Carmassi et al., 2013).

2.10. Chlorophyll a fluorescence

Measurements were carried out during the experiment utilizing a portable chlorophyll fluorometer (Handy Pea, Hansatech Instruments Ltd., UK) (Strasser et al., 2004). Three fully expanded leaves were dark-adapted using leaf clips (4 mm diameter) for 30 min and then exposed to an excitation light intensity (ultra-bright red LEDs with a peak at 650 nm) of 3000 μmol m^{-2} s^{-1} provided by three high-intensity light-emitting diodes. The parameter measured was the maximum quantum yield efficiency of primary PSII photochemistry (Fv/Fm) (Trivellini et al., 2023).

2.11. Total flavonoids content and antioxidant capacity

Frozen tomato leaf tissue (0.1 g) from three fully expanded leaves was homogenised in 5 mL of methanol, sonicated at low temperature for one hour, and subsequently left overnight under constant extraction conditions. After extraction, samples were centrifuged at 12,000 RCF for 15 min at 4 °C. For the determination of total flavonoid content, 0.1 mL of the resulting methanolic extract was mixed sequentially with 60 μL of 5 % sodium nitrite ($NaNO_2$), 40 μL of 10 % aluminium chloride ($AlCl_3$), followed by the addition of 0.4 mL of sodium hydroxide (NaOH) and 0.2 mL of distilled water after 5 min. Absorbance was measured at 510 nm using a spectrophotometer, and flavonoid content was expressed as mg of catechin equivalents (CAE) per gram of fresh weight (FW) (Kim et al., 2003).

Antioxidant activity was evaluated using the Ferric Reducing Antioxidant Power (FRAP) assay. In this procedure, 0.1 mL of the methanolic extract was added to 2 mL of sodium acetate buffer 0.25 M (pH3.6) and 0.9 mL of FRAP reagent, which consisted of 1 mM 2,4,6-tripyridyl-s-triazine (TPTZ) and 2 mM ferric chloride ($FeCl_3$) in 250 mM sodium acetate buffer (pH 3.6). The mixture was incubated at 20 °C for 4 min before absorbance was recorded at 593 nm. Ferrous ammonium sulfate $[(NH_4)_2Fe(SO_4)_2{\cdot}6\,H_2O]$ was used for calibration and results were expressed as micromoles of ferrous ion equivalents [Fe^{2+}] per gram of fresh weight (μmol Fe^{2+} g^{-1} FW) (Maggini et al., 2021).

2.12. Hormone concentration in leaves

For hormone profiling, leaf tissues from three fully expanded leaves were ground in liquid nitrogen with a mortar and stored at −80 °C until extraction. For each sample, 500 mg of frozen powder were incubated overnight (~24 h) at 4 °C in 5 mL of extraction solution (methanol: Milli-Q water: formic acid = 75: 20: 5, v/v/v) under gentle agitation. After the incubation, samples were sonicated for 10 min in a chilled ultrasonic bath, followed by an additional 10 min of cold ultrasonic bath. Extracts were centrifuged at 2000 RCF for 15 min and filtered through 0.2 μm Chromafil® Xtra PET-45/25 syringe filters (Macherey–Nagel, Düren, Germany) before analysis.

Quantification was performed by LC-MS/MS using a Sciex 5500 QTrap+ mass spectrometer (AB Sciex LLC, Framingham, MA, USA), equipped with a Turbo V ion-spray source and coupled to an ExionLC AC System custom-made by Shimadzu (Shimadzu Corporation, Kyoto, Japan) which includes ExionLC Controller, ExionLC Degasser, 2 ExionLC AC Pumps, ExionLC AC Autosampler. The UHPLC chromatographic separation for targeted quantification of hormones was performed on a Phenomenex Kinetex F5 LC column (2.6 μm, 100 × 2.1 mm, 100 Å; Phenomenex, Torrance, CA, USA). Chromatographic separation was conducted using a gradient elution system with solvent A (acetonitrile + 0.1 % formic acid) and solvent B (Milli-Q water + 0.1 % formic acid). The gradient programme was as follows: 5 % A at 0 min; linear increase to 95 % A from 0 to 10 min; maintained at 95 % A until 12 min, followed by re-equilibration at 5 % A for 4 min. The flow rate was set to 400 μL min^{-1}, with an injection volume of 20 μL and column oven temperature maintained at 40 °C.

The following phytohormones were analysed: salicylic acid (SA), indole-3-acetic acid (IAA), abscisic acid (ABA), zeatin (Z), gibberellic acids (GA_4), jasmonic acid (JA), melatonin (MEL), and metatopolin (MET). MS/MS detection was performed using electrospray ionisation (ESI) in negative mode for SA, IAA, JA, ABA and GA_4, and in positive mode for Z, MEL, and MET, with nitrogen used as the collision gas. MS parameters optimization has been carried out as described by Fidalgo-Illesca et al. (2025).

For phytohormones quantification, individual calibration curves were obtained by using multicomponent standard mixtures containing pure commercial standard references (Merck Group, Milan, Italy) for all the hormones considered. Ten-point calibration curves were prepared applying serial dilutions in the range 1–512 ppb.

2.13. Statistical analysis

Data were analysed using both PRISM 10.3.1 software (GraphPad Software, San Diego, CA, USA) and R version 4.4.2 (RStudio, PBC, Boston, MA, USA). Height (cm), dry weight (g), number of nodes and leaves of one *S. lycopersicum* cv and five S. *pimpinelluifolium* accessions in Salt and Non Salt conditions were analysed using PCA. Before PCA, the data were centered by subtracting the mean of each variable and the analysis was based on the covariance matrix. The number of principal components (PC) was determined by selecting those that explained at least 90 % of the total variance. To assess individual differences between cultivar/accessions under salt stress, unpaired two-tailed *t*-tests were conducted for each morphological variable ($p < 0.05$). Percentage data were arcsine-transformed to stabilise variance and improve normality. Two-way ANOVA was performed to assess the effects of treatment and accession/variety on *S. lycopersicum* L. and *S. pimpinellifolium* L., within the studied sampling time or to evaluate differences across treatments and species. Mean comparisons was carried out using the Tukey's HSD multiple comparison test ($p < 0.05$).

Hormone data were log-transformed [$\log(x + 1)$] and standardised (z-score) prior to analysis to normalise distributions. Permutational multivariate analysis of variance (PERMANOVA) and Canonical Analysis of Principal Coordinates (CAP) were conducted following Anderson and Willis (2003), using the vegan (Oksanen, 2022) and BiodiversityR (Kindt and Coe, 2005) packages in R. CAP analyses were performed separately at each sampling time to investigate species-specific differences in hormonal profiles based on Euclidean distances; ordination plots included 95 % confidence intervals.

Homogeneity of group dispersions was assessed with betadisper. Pairwise PERMANOVA comparisons with Benjamini–Hochberg correction was used to identify significant differences between groups. A heatmap of violaxanthin, lutein, total flavonoids, and antioxidant capacity was generated using the pheatmap package in R. Data were log-transformed [$\log(x + 1)$] and z-score standardised prior to plotting. Principal component analysis (PCA) was performed to reduce the dimensionality of the dataset and identify patterns between variables. Values are means of 3 independent biological samples.

3. Results

3.1. Preliminary screening of S. pimpinellifolium accessions under salinity stress

To identify the most salt-tolerant *S. pimpinellifolium* genotype, five accessions (WR2 – LYC2824, WR9 – LYC2794, WR10 – LYC2750, WR11 – LYC2665, and WR14 – LYC2914) were cultivated under 35 % seawater salinity in semi-controlled greenhouse conditions. Morphological traits (plant height, dry biomass, number of nodes, and number of leaves) were evaluated at the final sampling point. WR2, previously identified as the most salt-tolerant genotype in an *in vitro* screening (Cialli et al., 2025), confirmed its superior performance under *in vivo* conditions. Principal Component Analysis (PCA) based on morphological traits revealed a separation of WR2 from the other genotypes, highlighting its distinct growth profile under salinity stress (Fig. S1). Statistical comparisons further supported WR2's consistently higher tolerance (Tab. S1). Based on this combined *in vitro* and *in vivo* evidence, WR2 was selected for detailed physiological and hormonal analyses, in direct comparison with the salt-sensitive *S. lycopersicum* cv. 'Principe Borghese'. All results presented in the following sections refer specifically to the WR2 accession of *S. pimpinellifolium*.

3.2. Growth and yield reflect divergent stress response strategies

Morphological and yield parameters were initially evaluated to determine the impact of salinity on plant performance and productivity in the two tomato species under Salt and Non Salt conditions. Under salinity stress, both species exhibited a significant reduction in plant height (Fig. 1a) and fresh weight (Fig. 1b); however, *S. pimpinellifolium* L. showed a less pronounced decrease compared with *S. lycopersicum* L. A contrasting trend was observed in dry weight (Fig. 1c), where only *S. lycopersicum* exhibit significant reduction under salinity stress.

Full two-way ANOVA statistics (p-values for treatment, species, and their interaction) for all parameters studied in this work are provided in Supplementary Table S2.

Salinity also affected reproductive development, reducing the number of inflorescences per plant (Fig. 2a). Ten days after the onset of salt treatment, *S. pimpinellifolium* L. had initiated flowering under both experimental conditions, whereas *S. lycopersicum* L. had not yet developed inflorescences. *S. lycopersicum* L. showed an increase over time but produced consistently fewer inflorescences under salinity compared with control conditions. By the final time point, the commercial species under salt stress displayed a significantly lower number of inflorescences compared to the same species under control conditions, as well as to the wild species under both treatments. *Solanum lycopersicum* L. also showed a significant decrease in the weight of ten fruits per plant under salinity, whereas dry matter content (%) increased under salt stress in both species (Fig. 2b; Tab. S3). All fruits were harvested at the same ripening stage, selected using a portable colourimeter, to ensure consistency across treatments and genotypes. The corresponding colourimetric values are reported in Table S4. This trend was also evident from fruit images (Fig. 2c), where *S. pimpinellifolium* L. fruits appeared similar in size under both conditions, while *S. lycopersicum* L. fruits grown under saline irrigation were visibly smaller than those grown under optimal conditions. Salt reduced fruit firmness in *S. lycopersicum* L., while *S. pimpinellifolium* L. maintained stable values across treatments (Fig. 2d). As expected, salt stress increased total soluble solids (TSS) only in *S. lycopersicum* L. (Fig. 2e). In contrast, fruit acidity (Fig. 2f) remained stable in *S. lycopersicum* L. but declined under salinity in *S. pimpinellifolium* L. Regarding pigments (Fig. S2), *S. lycopersicum* L. accumulated significantly more lycopene under salt, with β carotene showing a non-significant upward trend. Conversely, *S. pimpinellifolium* L. maintained stable lycopene but exhibited a significant decrease in β carotene under stress.

3.3. Osmotic adjustment and ion regulation are involved in water status under salt stress

Osmolyte content (Fig. 3a) did not differ between species under control conditions. Under salinity, however, *S. pimpinellifolium* L. accumulated significantly higher osmolyte levels than *S. lycopersicum* L. at all time points. While *S. pimpinellifolium* L. maintained consistently elevated concentrations throughout the experiment, *S. lycopersicum* L. showed significant increases only at T3 and T4.

Electrolyte leakage (EL) (Fig. 3b) also differed between species. Under control conditions, *S. lycopersicum* L. exhibited significantly higher EL than *S. pimpinellifolium* L. from T1 to T3, with no difference at T4. Salinity increased EL in both species compared with their respective controls, but values were consistently higher in *S. lycopersicum* L., except at T3 where no significant differences were observed.

Ion ratios measured in leaves and roots and selective transport of ions over Na^+ at the end of the experiment (T4) are reported in Table 2. Under control conditions, both species exhibited low Na^+/K^+ and Na^+/Ca^{2+} ratios in leaves and roots, with no major differences between *S. lycopersicum* L. and *S. pimpinellifolium* L.. Salt treatment markedly

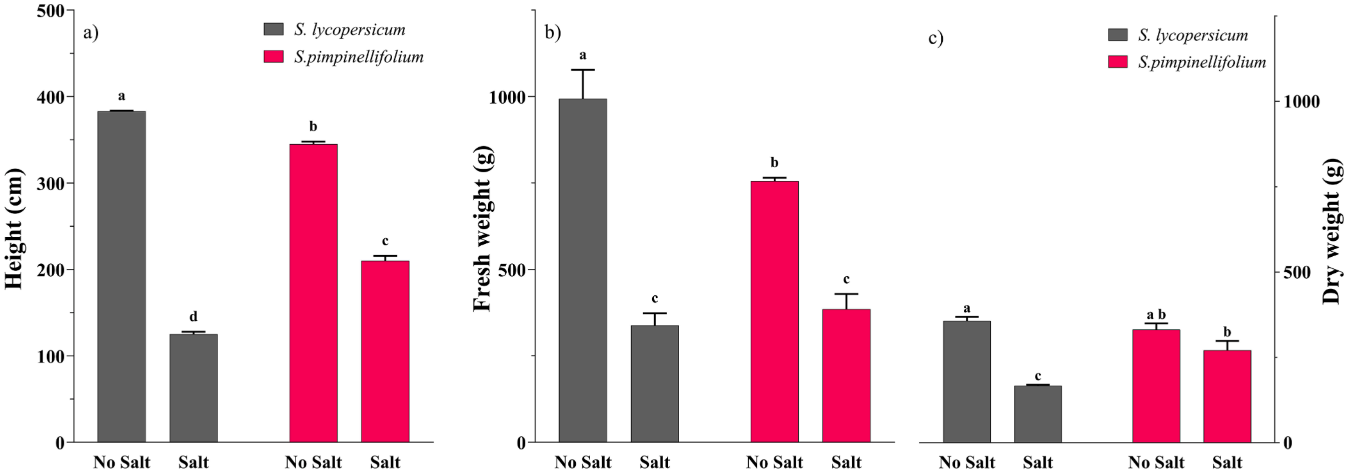


Fig. 1. Effect of salinity on growth parameters in *S. lycopersicum* L. and *S. pimpinellifolium* L.. (a) Plant height (cm), (b) fresh weight (g) and (c) dry weight (g) measured at the end of the experimental period (T4) in plants grown under control (Non Salt) and salinity stress (Salt) conditions. Data represent means ± SEM (n = 3). Different lowercase letters indicate significant differences between treatments and species ($p < 0.05$). Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test.

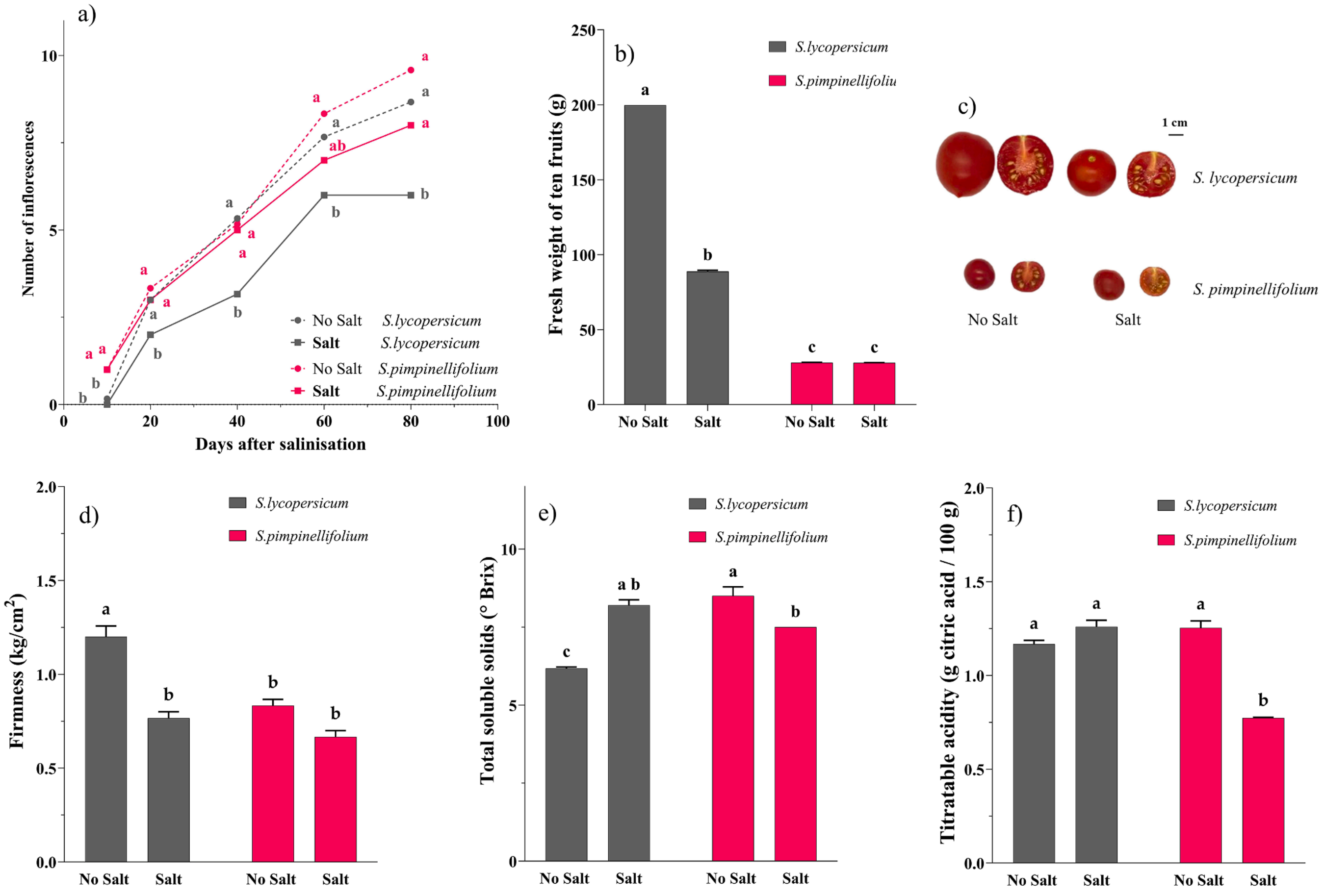


Fig. 2. Effect of salinity on yield and fruit quality parameters in *S. lycopersicum* L. and *S. pimpinellifolium* L.. (a) Progression of inflorescence number over time (days after transplanting), (b) fresh weight of ten fruits measured at harvest, (c) representative images of fruits from both species grown under control (Non Salt) and salinity stress (Salt) conditions – scale bar = 1 cm, (e) total soluble solids (°Brix) and (f) titratable acidity (g citric acid 100 g^{-1} fresh weight). Data represent means ± SEM (n = 3). Different lowercase letters indicate significant differences between treatments and species ($p < 0.05$). Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test; in (a) letters indicate differences within each sampling time, whereas in (b-e) they reflect differences across all treatments and species.

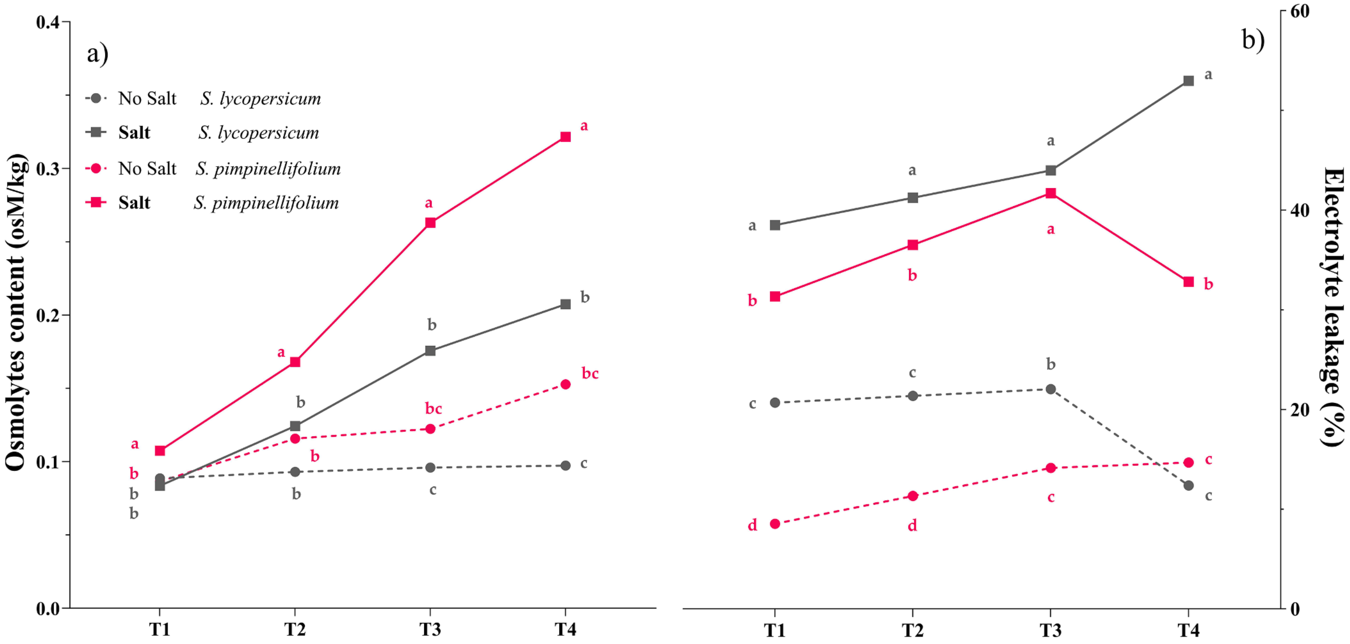


Fig. 3. Effect of salinity on osmotic, membrane damage and ionic parameters in *Solanum lycopersicum* L. and *S. pimpinellifolium* L.. (a) Osmolyte content (osM/kg) and (b) electrolyte leakage (percentage) measured at four time points (T1–T4) during the experimental period. Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test. Different lowercase letters indicate significant differences between treatments and species within each sampling time ($p < 0.05$).

increased these ratios in both species, but with distinct patterns between organs and genotypes. In leaves, *S. lycopersicum* L. showed the highest Na^+/K^+ and Na^+/Ca^{2+} ratios under salinity, significantly exceeding those of *S. pimpinellifolium* L., conversely, in roots, *S. pimpinellifolium* L. displayed significantly higher Na^+/K^+ and Na^+/Ca^{2+} ratios compared with *S. lycopersicum* L. Selective transport of ions over Na^+ was significantly reduced under salt stress, with the lowest values recorded in *S. lycopersicum* L.

RWC was measured at the final sampling point (T4) (Fig. S3). No significant differences were observed between Salt and Non Salt conditions in *S. pimpinellifolium* L.. In *S. lycopersicum* L., RWC values were significantly lower under Salt compared to Non Salt conditions.

3.4. *Changes of photoprotective compounds and antioxidant defences under salinity*

Chlorophyll content and selected photoprotective and antioxidant compounds were assessed at the final sampling point (T4) (Fig. 4). Total chlorophyll (Fig. 4a) decreased significantly in *S. lycopersicum* L. under Salt compared with Non Salt, whereas *S. pimpinellifolium* L. showed no significant change. The heatmap (Fig. 4b) summarises the normalised levels of violaxanthin, lutein, total flavonoids, and antioxidant capacity, with statistical significance reported in Table S5. Violaxanthin content was lowest in *S. lycopersicum* L. under Non Salt, while all other treatments showed higher, statistically comparable values. Lutein increased under salinity in both species, reaching the highest concentration in *S. pimpinellifolium* L. Antioxidant capacity was lowest in *S. lycopersicum* L. under Salt and in *S. pimpinellifolium* L. under Non Salt, as indicated by darker blue shades in the heatmap, whereas all other conditions displayed higher values. For total flavonoids, the lowest levels occurred in stressed *S. lycopersicum* L., while the highest were detected in *S. lycopersicum* L. under Non Salt and *S. pimpinellifolium* L. under Salt, with intermediate values in *S. pimpinellifolium* L. under Non Salt.

3.5. *Leaf functionality under stress*

The maximum quantum efficiency of photosystem II (Fv/Fm) and stomatal conductance were analysed to evaluate the impact of salinity on leaf functionality. Fv/Fm (Fig. 5a), assessed at T4, did not show statistically significant differences between the two species under saline conditions. Nonetheless, *S. lycopersicum* displayed a consistent decline in Fv/Fm across all sampling time points compared with its control, whereas values in *S. pimpinellifolium* remained stable (Fig. S4). In contrast, stomatal conductance (Fig. 5b) significantly decreased in both species, with a more pronounced reduction in *S. pimpinellifolium* than in *S. lycopersicum* under salt stress. To clearly illustrate the impact of salinity on leaf functionality, only the final measurement (T4) for both measurements is presented in the main figure (Fig. 5).

Hormonal dynamics of *S. lycopersicum* L. and *S. pimpinellifolium* L. during Salt Stress

Permutational multivariate analysis of variance (PERMANOVA) and Canonical Analysis of Principal coordinates (CAP) were used to assess the effects of species and treatment on the hormonal profiles of *S. lycopersicum* L. and *S. pimpinellifolium* L. across four time points (T1, T2, T3, T4), (Fig. 6). PERMANOVA revealed a highly significant effect of treatment at all sampling times ($p \leq 0.001$), consistently explaining the largest proportion of variance in the dataset (Tab. S7). CAP analysis confirmed a clear separation between species and treatments over time. Ordination plots of the linear discriminants (LD1 and LD2) showed distinct clustering of the two species at each time point (Fig. 6a–d). Within each species, Salt and Non Salt conditions also formed separate groups with minimal or no overlap. Classification accuracy based on CAP (Tab. S6) supported these patterns: 100 % of samples were correctly assigned to species at T1, T3, and T4. At T2, classification remained complete for *S. lycopersicum* L., while a slight reduction was observed in *S. pimpinellifolium* L. (83.33 %).

To further characterise the hormone profiles underlying the observed multivariate patterns, individual hormone levels across species, treatments, and time points was taken in consideration. The heatmap (Fig. 7) describes the normalised levels of all the hormones studied, while statistical significance reported in Table S. 7. ABA levels (Fig. 7a) at the first sampling point (T1) were higher in *S. pimpinellifolium* L. under Salt condition compared with all other conditions. At T2, no significant differences were observed between treatments or species. By T3, both

Table 2
Table shows values of selective transport (ST) of K^+, Mg^{2+} and Ca^{2+} over Na^+, Na^+/K^+ and Na^+/Ca^{2+} measured on leaves and roots of *S. lycopersicum* L. and *S. pimpinellifolium* L. in Salt and Non Salt conditions at the end of the experiment. Different lowercase letters indicate significant differences between treatments and species ($p < 0.05$). Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test.

Species	Treatment	ST	Na^+/K^+ leaves	Na^+/K^+ roots	Na^+/Ca^{2+} leaves	Na^+/Ca^{2+} roots
S. lycopersicum L.	Non Salt	1,16 ± 0,02 b	0,06 ± 0,01 c	0,27 ± 0,04 c	0,46 ± 0,08 c	1,81 ± 0,35 c
S. lycopersicum L.	Salt	0,82 ± 0,01 d	2,24 ± 0,22 a	0,69 ± 0,09 b	2,42 ± 0,16 a	5,58 ± 0,21 b
S. pimpinellifolium L.	Non Salt	1,07 ± 0,01 c	0,09 ± 0,00 c	0,17 ± 0,01 c	0,23 ± 0,03 c	0,85 ± 0,21 d
S. pimpinellifolium L.	Salt	1,23 ± 0,03 a	0,81 ± 0,02 b	0,96 ± 0,05 a	1,36 ± 0,07 b	6,49 ± 0,16 a

species showed higher ABA concentrations under Non Salt condition. By the end of the experiment (T4), *S. lycopersicum* L. under Non Salt recorded the highest ABA level, significantly exceeding all other treatments, which did not differ from each other. At T1, salicylic acid (SA) content (Fig. 7b) did not differ between species under Non Salt conditions. Under salt stress, both species exhibited increased SA levels, with *S. lycopersicum* L. initially displaying significantly higher values than *S. pimpinellifolium* L.. At T2, no differences were observed between species under control conditions; however, salt treatment induced a significant increase in both species, with *S. pimpinellifolium* L. exhibiting higher SA levels than *S. lycopersicum* L. This pattern persisted at T3, although *S. pimpinellifolium* L. under control conditions and *S. lycopersicum* L. under salt stress exhibited comparable SA levels. At the final time point (T4), *S. pimpinellifolium* L. under salt stress displayed the highest SA concentration. Intermediate levels were observed in *S. pimpinellifolium* L. under control and *S. lycopersicum* L. under salt, with no significant differences between them. The lowest SA levels were recorded in *S. lycopersicum* L. under control, which did not differ significantly from the same species under salt stress. Z levels (Fig. 7c) did not differ significantly between species under Non-Salt conditions throughout the experiment. At T1 and T2, *S. lycopersicum* showed higher concentrations of this hormone than *S. pimpinellifolium*, although the differences were not statistically significant. In the second part of the experiment (T3 and T4), both species exhibited increased Z levels compared with their respective controls. At T3, *S. pimpinellifolium* displayed higher values than *S. lycopersicum*, without significant differences, while at T4 *S. pimpinellifolium* showed a marked rise in Z concentration, reaching levels higher than those observed under the other conditions. Metatopolin levels (Fig. 7d) did not differ significantly between species under Non Salt conditions at any time point. In *S. lycopersicum* L., Salt treatment generally resulted in lower metatopolin concentrations compared to Non Salt, except at the final sampling time (T4), when levels increased significantly. In contrast, *S. pimpinellifolium* L. showed significantly higher metatopolin levels under Salt compared to Non Salt at both T3 and T4. IAA levels were reported in Fig. 7e. At the first sampling point (T1), *S. pimpinellifolium* L. under salt stress exhibited lower IAA levels than under control, whereas no differences were observed in *S. lycopersicum* L. At T2, *S. lycopersicum* L. under salt displayed higher IAA levels compared with control, while *S. pimpinellifolium* L. showed no significant changes. At T3, no treatment differences were detected within each species, but *S. lycopersicum* L. maintained higher IAA levels than *S. pimpinellifolium* L. under both conditions. By the end of the experiment, *S. lycopersicum* L. exhibited a reduction in IAA under salt stress relative to control, whereas no significant differences were observed in *S. pimpinellifolium* L.. GA4 levels (Fig. 7f) didn't show differences between treatments or species at the beginning of the experiment. At T2, no significant differences were detected between the two species under Non Salt conditions. Both control treatments demonstrated higher GA4 levels than the Salt treatments, which did not differ significantly from each other. At T3, *S. lycopersicum* L. reduced GA4 levels in the presence of salt compared to the absence of salt, while in *S. pimpinellifolium* L. no significant differences were observed between treatments. At T4, *S. lycopersicum* L. under Salt condition decreased GA4 levels compared to the Non Salt condition, whereas *S. pimpinellifolium* L. maintained similar levels across treatments. JA levels are shown in Fig. 7g. At T1, both species showed significantly higher JA concentrations under Non Salt conditions compared to Salt, with no differences between species within the same treatment. At T2, *S. lycopersicum* showed an increase in JA content compared with its control, whereas in *S. pimpinellifolium* no significant differences were detected between salinity-stressed and control conditions. At T3 and T4, both species again recorded higher JA levels under Non Salt conditions compared to Salt, and within each time point, no significant differences were observed between species under the same treatment. Melatonin levels (Fig. 7h) did not differ between species at T1, although both exhibited higher concentrations under salt stress

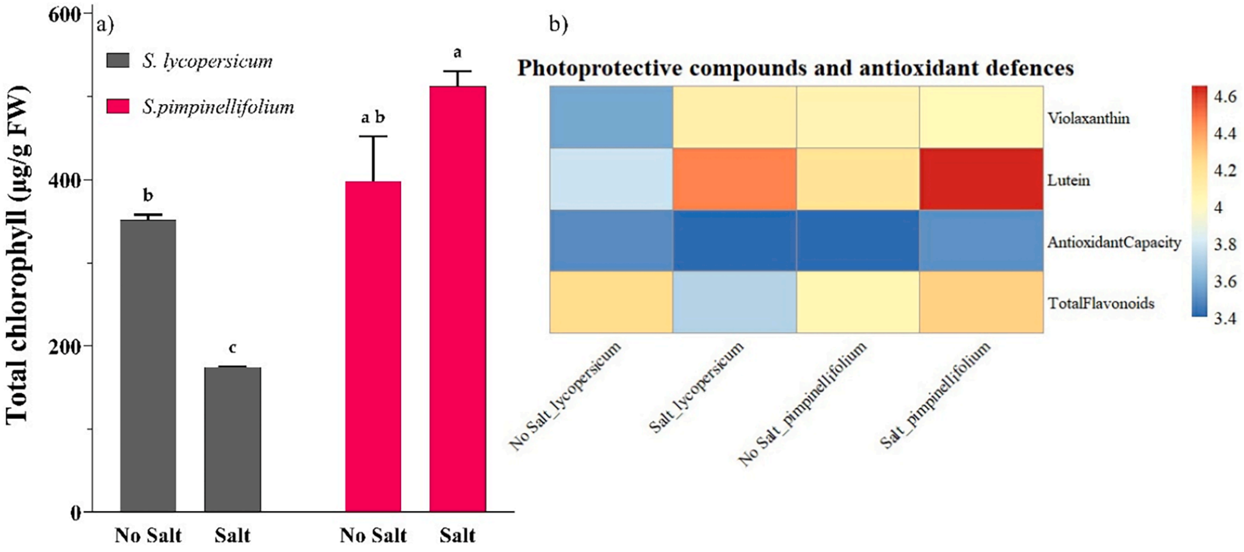


Fig. 4. Effect of salinity on chlorophyll content, photoprotective compounds and antioxidant defences in *Solanum lycopersicum* L. and *S. pimpinellifolium* L.. (a) Total chlorophyll content (μg g^{-1} fresh weight) measured at the end of the experimental period in plants grown under control (Non Salt) and salinity stress (Salt) conditions. Data represent means ± SEM (n = 3). Different lowercase letters indicate significant differences between treatments and species ($p < 0.05$). Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test. (b) Heatmap shows relative levels of violaxanthin, lutein, total flavonoids and antioxidant capacity in the two species under control and salinity stress. The heatmap colour scale represents relative concentration values, with red indicating higher levels and blue lower levels. Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test, as reported in Supplementary Table S5.

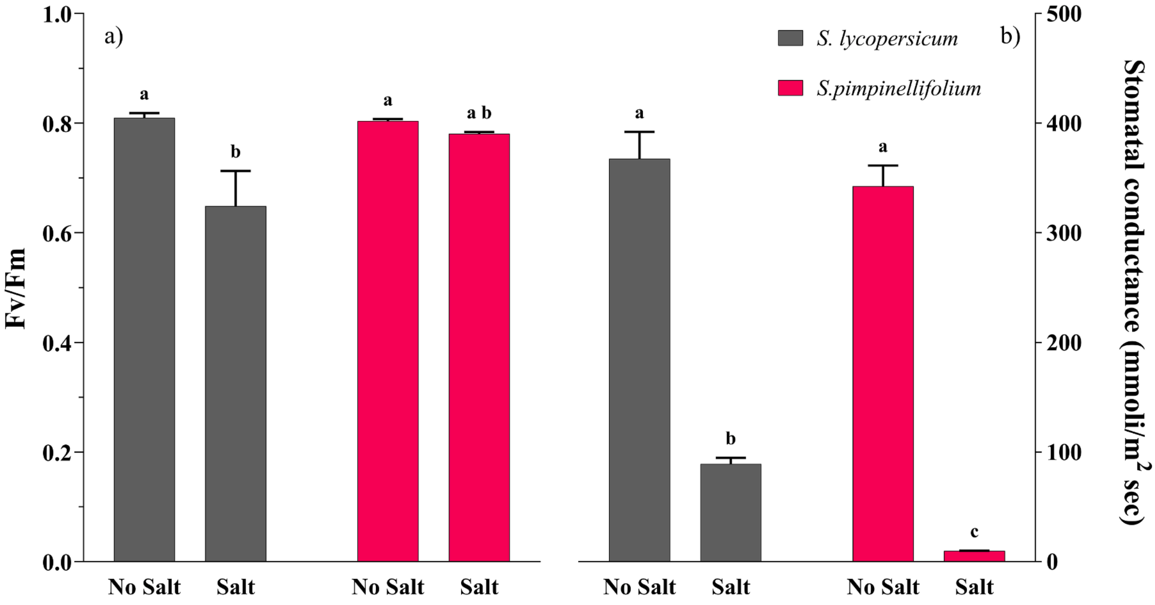


Fig. 5. Effect of salinity on stomatal conductance and photosystem II efficiency in *Solanum lycopersicum* L. and *S. pimpinellifolium* L.. (a) maximum quantum efficiency of photosystem II (Fv/Fm) and (b) Stomatal conductance (mmol m^{-2} s^{-1}) measured at the end of the experimental period in plants grown under control (Non Salt) and salinity stress (Salt) conditions. Data represent means ± SEM (n = 3). Different lowercase letters indicate significant differences between treatments and species ($p < 0.05$). Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test.

compared with control. At T2, salt treatment continued to increase melatonin levels in both species, with *S. pimpinellifolium* L. under control displaying intermediate values not significantly different from the salt-treated groups. At T3, *S. pimpinellifolium* L. under salt showed the highest melatonin concentration, significantly exceeding all other conditions, while *S. lycopersicum* L. also exhibited elevated levels under salt compared to control. This pattern persisted at T4, with salt-treated *S. pimpinellifolium* L. further increasing melatonin content, whereas all other treatments remained significantly lower.

4. Discussion

This comparative study revealed distinct physiological and morphological strategies underlying salinity tolerance in *S. pimpinellifolium* and *S. lycopersicum*, highlighting traits that contributes to the wild species' superior tolerance. Among the mechanisms contributing to the resilience of *S. pimpinellifolium*, hormonal regulation emerged as a major physiological component, coordinating growth, osmotic adjustment, and stress protection within a broader regulatory network. Given that salinity tolerance relies on maintaining both vegetative (Munns and Tester, 2008) and reproductive performance

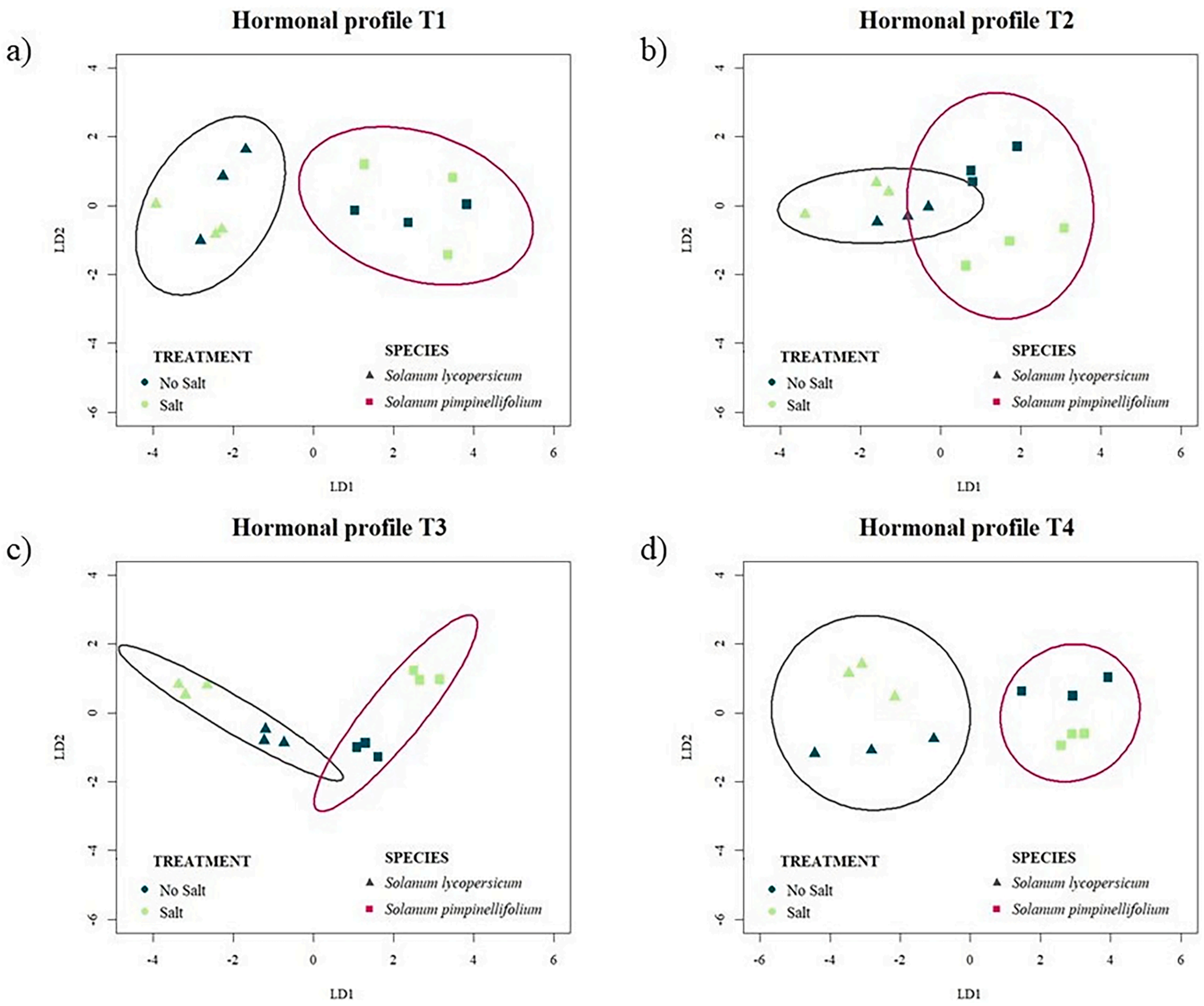


Fig. 6. Effect of salinity on hormonal profile in *Solanum lycopersicum* L. and *S. pimpinellifolium* L.. Linear discriminant (LD) plots from Canonical Analysis of Principal coordinates (CAP) based on all hormones analysed measured at (a) T1, (b) T2, (c) T3 and (d) T4. (a). The ellipses identify the clustering of the two species (*S. lycopersicum* L., in grey and *S. pimpinellifolium* L., in purple), while the coloured dots identify the two treatments (Non Salt, in dark blue and Salt, in light green). Each ellipse represents the 95 % confidence interval.

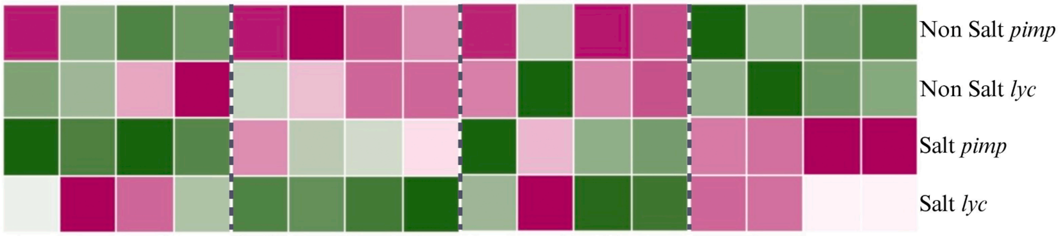
(Agius et al., 2022), morphological and yield traits were examined, revealing clear differences under identical stress conditions.

Under salinity, *S. lycopersicum* L. showed strong growth inhibition and reduced biomass (Fig. 1) and fruit yield (Fig. 2) (Maggio et al., 2007), whereas *S. pimpinellifolium* L. was more resilient, with smaller reductions in weight and height (Rao et al., 2013) and no decline in dry weight (Fig. 1), a key indicator of tolerance (Morton et al., 2024).

Salinity also affected reproductive development (Fig. 2), particularly flowering. In *S. lycopersicum*, stress delayed flowering and reduced the number of inflorescences, whereas *S. pimpinellifolium* maintained both onset and progression. This divergence reflects a phenological shift adopted by *S. lycopersicum* and commonly observed under salt stress, enabling plants to complete reproduction before excessive salt accumulation (Takeno, 2011; Sun et al., 2024). The ability of *S. pimpinellifolium* to preserve its flowering schedule indicates a plastic and adaptive phenological programme (Monforte, 2020) that supports reproductive stability and yield maintenance under saline conditions.

These differences extended to fruit production (Fig. 2): salinity reduced fruit number, size, and firmness more in *S. lycopersicum* L. than in the wild species (Martínez-Cuenca et al., 2020). Fruit fresh weight decreased in *S. lycopersicum* L. but remained stable in *S. pimpinellifolium* L., despite both showing higher dry matter. In the cultivated species, this was coupled with increased sugars and acids, driving a typical rise in total soluble solids (TSS) under salt stress (Agius et al., 2022). In *S. pimpinellifolium* L., however, dry matter accumulation was not accompanied by higher sugars or acids, and TSS even declined, a pattern also observed in *S. chilense* (Martinez et al., 2012). This could suggest that carbon in the wild species was redirected from fruits towards osmoprotectants and stress-related metabolites in vegetative tissues, supporting adaptation rather than fruit-centred osmotic adjustment. In cultivated tomatoes, the classical increase in TSS under salinity (often with stable acidity) can enhance the perception of sweetness and overall flavour intensity (Cela et al., 2024; Agius et al., 2022). Conversely, the decline in both TSS and acidity in *S. pimpinellifolium* may reflect carbon diversion towards protective metabolites in leaves, potentially attenuating fruit flavour (Martínez-Cuenca et al., 2020). Fruit parameters were analysed as indicators of carbon allocation, sink strength and reproductive resilience under prolonged salinity, since variations in TSS, acidity and pigment reflect source-sink rebalancing and metabolic adjustment supporting osmotic regulation (Agius et al., 2022; Song

a) Abscisic acid b) Salicylic acid c) Zeatin d) Metatopolin



e) Indole -3-acetic acid f) Gibberellic acid 4 g) Jasmonic acid h) Melatonin

Fig. 7. Effect of salinity on leaf hormonal content in *Solanum lycopersicum* L. and *S. pimpinellifolium* L measured at four time points (T1–T4) during the experimental period in plants under control (Non Salt) and salinity stress (Salt) conditions. Heatmap shows relative levels of (a) Abscisic acid, (b) Salicylic acid, (c) Zeatin, (d) Metatopolin, (e) Indole −3-acetic acid, (f) Gibberellic acid 4, (g) Jasmonic acid, (h) Melatonin. Statistical significance was assessed using two-way ANOVA followed by Tukey's HSD test, as reported in Supplementary Table S8.

et al., 2022).

Reduced acidity in *S. pimpinellifolium* L. under salinity may reflect carbon diversion from citrate/malate pools to stress metabolism (Song et al., 2022; Yin et al., 2010). Pigment profiles followed a similar trend (Fig. S2): salinity increased lycopene in *S. lycopersicum* L. (Massaretto et al., 2018), whereas *S. pimpinellifolium* L. maintained stable lycopene but reduced β carotene, suggesting a shift from pigment synthesis to stress-responsive pathways.

Salt stress, driven by excessive sodium in the soil solution, imposes osmotic stress and ionic imbalance, impairing water uptake and cellular homeostasis (Guo et al., 2022). Species responses were assessed through osmolyte content, electrolyte leakage (EL%) (Fig. 3), and relative water content (RWC%) (Fig. S3) as indicators of osmotic adjustment and membrane stability. Both species increased osmolytes under stress (Anjum et al., 2023), but in *S. pimpinellifolium* L. this occurred from the start, sustaining RWC% (Patanè et al., 2022), whereas in *S. lycopersicum* L. reduced RWC% was coupled with higher EL% (Hniličková et al., 2019). As the plasma membrane is a primary target of salt-induced damage, EL is a common indicator of membrane stability, typically rising in sensitive species (Singh et al., 2023). Consistently, *S. pimpinellifolium* L. showed lower EL under both control and stress, indicating greater cellular integrity and effective osmotic adjustment.

Ion homeostasis further distinguished the two species (Table 1). Under salinity, *S. lycopersicum* L. showed higher Na$^+$/K$^+$ and Na$^+$/Ca^{2+} ratios in leaves—hallmarks of ionic toxicity and poor sodium exclusion (Wu, 2018). *Solanum pimpinellifolium* L., by contrast, maintained low leaf ratios while accumulating Na$^+$ mainly in roots, suggesting efficient vacuolar sequestration via Na$^+$/H$^+$ antiporters to preserve K$^+$-dependent metabolism (Apse et al., 1999; Rahnama et al., 2011). This pattern, possibly supported by phloem-mediated Na$^+$ recirculation (Tester, Davenport, 2003), was accompanied by lower root Na$^+$/Ca^{2+} under Salt, indicating greater Ca^{2+} availability for SOS-mediated Na$^+$ extrusion (Hadi and Karimi, 2012). Moreover, *S. pimpinellifolium* L. displayed more efficient selective transport of K$^+$, Ca^{2+} and Mg^{2+} over Na$^+$, ensuring retention of essential ions in leaves while restricting sodium to roots, thereby protecting photosynthetic tissues (Liang et al., 2024).

Leaf functional traits at T4, including PSII efficiency (Fv/Fm) and stomatal conductance (Fig. 5), confirmed contrasting strategies (Zhang et al., 2022b). *S. pimpinellifolium* L. preserved high PSII efficiency under stress, linked to strong stomatal closure, increased chlorophyll and lutein, and stable violaxanthin, maintaining a robust carotenoid pool (Fig. 4) (Young, 1991). Together with elevated flavonoids and antioxidant capacity, these traits form an integrated defence system that mitigates oxidative stress and supports photosynthesis, likely reinforced by early osmolyte synthesis and hormonal regulation (Hussain et al., 2024). By contrast, *S. lycopersicum* L. showed declines in chlorophyll and PSII efficiency, only modest carotenoid and flavonoid increases, and decreased antioxidant capacity. Weaker stomatal regulation and antioxidant defences likely contributed to greater water loss and membrane damage (Hedrich and Shabala, 2018).

Together, these morphological and physiological adjustments demonstrate the capacity of *S. pimpinellifolium* to maintain growth and reproductive functioning under prolonged salinity through coordinated phenological and osmotic responses. These results indicate that its superior tolerance is closely associated with efficient osmotic adjustment and ion homeostasis that preserve water balance and cellular integrity. Given the pronounced differences in physiological and morphological responses, it was important to determine whether these traits were underpinned by distinct hormonal dynamics. No previous work has provided a comprehensive, multi-faceted characterisation of hormonal regulation in *S. pimpinellifolium* under salt stress, making this comparison particularly relevant for understanding the hormonal basis of its superior tolerance.

Hormones act as central integrators of environmental signals, coordinating rapid stress perception with longer-term adjustments in growth and metabolism (Peleg and Blumwald, 2011; Verma et al., 2016). Analysis of the hormonal profiles of the two species revealed distinct patterns that may account for the ability of *S. pimpinellifolium* L. to sustain leaf functionality under salt stress, in contrast to the decline observed in *S. lycopersicum* L. multivariate analyses (Fig. 6; Tab S7) confirmed that salt stress exerted a strong influence on hormone profiles in both species, with ordination plots showing a clear separation between them, indicating that each follows a distinct strategy maintained throughout the experimental period (Zhang et al., 2022c).

The contrasting temporal profiles of ABA and cytokinins (zeatin and metatopolin) described in Fig. 7 between *S. pimpinellifolium* L. and

S. lycopersicum L. point to a coordinated hormonal strategy underpinning the wild species' superior salt tolerance. In *S. pimpinellifolium* L., salt stress triggered marked accumulation and sustained accumulation of abscisic acid (ABA), significantly higher than in *S. lycopersicum* L. at the onset of stress measurement (T1). ABA is a central regulator of plant salinity responses, promoting stomatal closure to limit water loss via transpiration and coordinating downstream gene expression to support osmotic adjustment and broader stress tolerance (Yoshida et al., 2014a, 2014b,2014c; Pardo-Hernández et al., 2024). Consistent with previous studies, sustained ABA accumulation under prolonged salinity contributes to maintaining water balance and photosynthetic stability (Sah et al., 2016; Yoshida *et al.*, 2019). This hormonal activation in the wild species likely underpins the stable relative water content (Fig. S3) and stomatal regulation (Fig. 5b) recorded in our physiological measurements at the end of the experiment, helping to preserve leaf functionality. Similar associations between timely ABA signalling and increased tolerance to abiotic stresses have been documented in other tomato genotypes and in several crop species (Soma et al., 2021; Holsteens et al., 2022). These associations are mechanistically coherent with genetic evidence showing that overexpression of the tomato of ABA-responsive element *SlAREB1* transcription factor, have been shown to enhance tolerance to salinity and drought by maintaining PSII efficiency, membrane integrity, and tissue water content (Hsieh et al., 2010). Conversely, loss or inhibition of ABA-dependent SnRK2–AREB/ABF signalling disrupted stomatal control and osmotic adjustment through downstream repression of ABA-responsive gene expression (Yoshida et al., 2014a,2014b,2014c). In addition to leaf level regulation, grafting studies have shown that root-derived ABA can strongly influence shoot physiology through root–shoot signalling. In tomato, constitutive overproduction of ABA in rootstocks enhances ABA transport to scion reproductive tissues and modifies leaf ABA catabolism and phloem ABA levels, demonstrating that ABA acts both locally and systemically to support performance under salinity (Martínez-Andújar et al., 2021).

This was followed by a subsequent increase in cytokinins, which exerted an opposite regulatory influence and coincided with stable chlorophyll content, enhanced photoprotective and antioxidant traits and reproductive development in *S. pimpinellifolium*, consistent with cytokinin-mediated maintenance of photosynthetic competence. In the present study, cytokinins—specifically zeatin and metatopolin (Fig. 7c, d)—exhibited distinct patterns between the two species under abiotic stress, with zeatin showing pronounced increases under salt stress, particularly in *S. pimpinellifolium* L. toward the end of the experiment. At T1 and T2, however, *S. lycopersicum* showed slightly higher zeatin levels than *S. pimpinellifolium* in stress condition, though not significantly. This transient rise may reflect a short-lived cytokinin response typical of sensitive genotypes (Zwack and Rashotte, 2015), contrasting with the later sustained increase in the wild species that supported pigment stability and photosynthetic maintenance. Metatopolin, in particular, has gained attention for its ability to delay leaf senescence, stabilise photosynthetic pigments, and modulate antioxidant responses under abiotic stress (Dobránszki, Mendler-Drienyovszki, 2014). These properties, together with the documented ability of cytokinins to sustain sink strength and meristem activity, could provide a strategic advantage in maintaining leaf functionality and reproductive output under salinity. Beyond their classical role in cell division and sink strength, cytokinins are increasingly recognised as modulators of photosynthetic capacity and pigment stability under stress. Their accumulation in the wild species under prolonged salinity may therefore help sustain chlorophyll content (Talla et al., 2016), enhance carotenoid and flavonoid levels (Kurepa et al., 2023), and preserve the functionality of the photosynthetic machinery even under extended stress conditions (Hudeček et al., 2023). In tomato, the constitutive overexpression of the isopentenyltransferase 3 (*SlIPT3*) gene (35S::*SlIPT3*), a key enzyme involved in cytokinin biosynthesis, enhanced salt tolerance by maintaining chlorophyll and carotenoid levels, increasing K^+/Na^+ ratios, and enhancing growth under salinity (Žižková et al., 2015). Similarly, root-localized *IPT* expression elevates cytokinin fluxes, leading to improved ion homeostasis and yield in salinized tomato plants (Ghanem et al., 2011).

This sequential and opposing regulation between ABA and cytokinins in *S. pimpinellifolium* L. might contribute to balancing initial stress protection with the maintenance of photosynthetic performance and yield under salinity conditions (Zwack and Rashotte, 2015). In contrast, the delayed increase in ABA and the weaker cytokinin response observed in *S. lycopersicum* L. may have contributed to suboptimal stomatal regulation, premature pigment loss, and reduced reproductive performance. This was reflected in greater reductions in plant height and biomass, delayed flowering onset, and fewer inflorescences compared with *S. pimpinellifolium* L., which maintained more stable growth, initiated flowering earlier, and sustained reproductive development throughout the experiment.

Auxin (IAA) and gibberellin (GA4) (Fig. 7e, f), both central to cell elongation, organ development, and reproductive progression (Yu et al., 2020), exhibited clear species-specific patterns under salinity. Even under control conditions, baseline IAA levels differed between species, reflecting the strong genotype-dependence of auxin homeostasis reported in tomato and other crops (Salehin, 2024). In *S. lycopersicum*, IAA levels fluctuated markedly across sampling points and treatments, suggesting instability in developmental signalling under stress. By contrast, *S. pimpinellifolium* L. maintained more stable auxin levels, with a moderate reduction under salinity that aligns with literature indicating that salt-tolerant genotypes often down-regulate IAA to balance growth restraint with stress acclimation (Gonzales and Kelley, 2025). This modulation may help limit excessive elongation while preserving essential developmental processes. At the transcriptional level, salt stress represses key IAA signalling genes (ARF, SAUR) and modulates auxin biosynthetic enzymes (CYP83B1, UGT74B1), could be consistent with the hormonal fluctuations observed in *S. lycopersicum* (Wang et al., 2023). Instead, a more buffered transcriptional control of auxin synthesis and transport could support the stable IAA pattern recorded in *S. pimpinellifolium* under stress.

GA4 profiles followed a similar divergence. In *S. lycopersicum* L., concentrations declined suddenly under salinity, particularly at later stages, corresponding with reduced plant height and biomass (Fig. 1) and the inability to sustain flowering (Fig. 2) (Serrani et al., 2007). Conversely, *S. pimpinellifolium* L. sustained relatively stable GA4 levels across treatments, consistent with its earlier flowering, sustained inflorescence production, and reduced growth penalties under stress as reported for *Arabidopsis thaliana* by Mutasa-Göttgens and Hedden (2009). Comparable patterns, where stable GA supply supports reproductive resilience in salt-tolerant species, have been documented in rice and wheat (Colebrook et al., 2014).

In the wider hormonal context, the stability of IAA and GA4 in *S. pimpinellifolium* L. complements the initial peak of ABA and the subsequent increase in cytokinin, forming a coordinated network that balances growth regulation with stress protection (Verma et al., 2016). This integration appears to safeguard both vegetative and reproductive development, whereas in *S. lycopersicum* L. the combined effects of unstable auxin signalling and declining GA4 may exacerbate the impacts of suboptimal ABA-cytokinin regulation, leading to more severe growth and yield penalties observed under salinity conditions (Fahad et al., 2015).

Although not a classical phytohormone, melatonin has emerged as a key regulator of plant stress responses, displaying signalling functions comparable to hormonal pathways (Yang et al., 2022). In tomato, overexpression of *SlCOMT1* enhances melatonin accumulation and salt stress resistance, while genetic manipulation of *COMT* and *GSNOR* demonstrates that boosting melatonin–nitric oxide crosstalk improves saline–alkali tolerance (Liu et al., 2019). These genetic findings support the view that melatonin functions as both a signal and effector molecule in stress acclimation, a concept consistent with its physiological roles observed in the present study. Notably, melatonin directly scavenges ROS and helps maintain ionic homeostasis under salt stress by modulating ion transporters (Liu et al., 2020). Melatonin also promotes the accumulation of osmoprotectants, thereby helping to stabilise osmotic balance and protecting cells from oxidative damage (Yusuf et al., 2024). In addition to its antioxidant activity (Siddiqui et al., 2020), melatonin has been shown to support plant growth and chlorophyll biosynthesis under stress conditions and to enhance photosynthetic capacity and photoprotection, thereby improving salt tolerance (Chen and Arnao, 2022). Moreover, phytomelatonin can regulate primary and secondary metabolism, influencing pigment biosynthesis and phenolic accumulation (Tan et al., 2012). In *S. pimpinellifolium* L., the highest concentration of melatonin was recorded at the end of the experiment (Fig. 7h), coinciding with sustained leaf functionality (Fig. 5) and an increase in antioxidant compounds and activity (Fig. 4). These multifaceted actions of melatonin are consistent with the physiological traits described above, suggesting an important role for this phytoregulator. In wild tomatoes, melatonin might not only directly protect the photosynthetic machinery but also support pigment stability, ion homeostasis, and osmoprotectant synthesis, indicating a potential basis for the superior capacity of this species to cope with salt stress.

Regarding SA, *S. lycopersicum* exhibited a sharper increase in its endogenous content than *S. pimpinellifolium* only at T1, suggesting a possibly transient activation of defence signalling (Fig. 7b). In contrast, the progressive and sustained SA accumulation observed in the wild species over time points (T2–T4) likely reflects a more controlled and enduring regulatory response to salinity. This result is consistent with the well-known role of SA as a stress-signalling hormone that enhances salt tolerance (El-Esawi et al., 2017). Under saline stress conditions, this phytohormone can ameliorate photosynthetic inhibition by improving CO_2 fixation and preserving Rubisco carboxylation (Lee et al., 2014). Additionally, SA mitigated oxidative damage, as demonstrated by Karimi et al. (2025), who observed lower malondialdehyde (MDA) levels in SA-treated plants, indicating reduced lipid peroxidation. These dynamics were consistent with the maintenance of photosynthetic efficiency observed in *S. pimpinellifolium* L. under stress conditions (Fig. 5). Consistent with recent transcriptomic evidence in *Brassica* spp. (Gulzar et al., 2025), SA enhances the transcription of Na^+/H^+ antiporter (NHX) genes and antioxidant pathways, strengthening ionic homeostasis and ROS detoxification under salinity. Such transcriptional activation may underlie the greater physiological stability observed in the wild species.

JA exhibited a distinctive pattern (Fig. 7g), with concentrations generally higher under control conditions at most sampling points and only a transient increase under salt stress at T2. This observation is

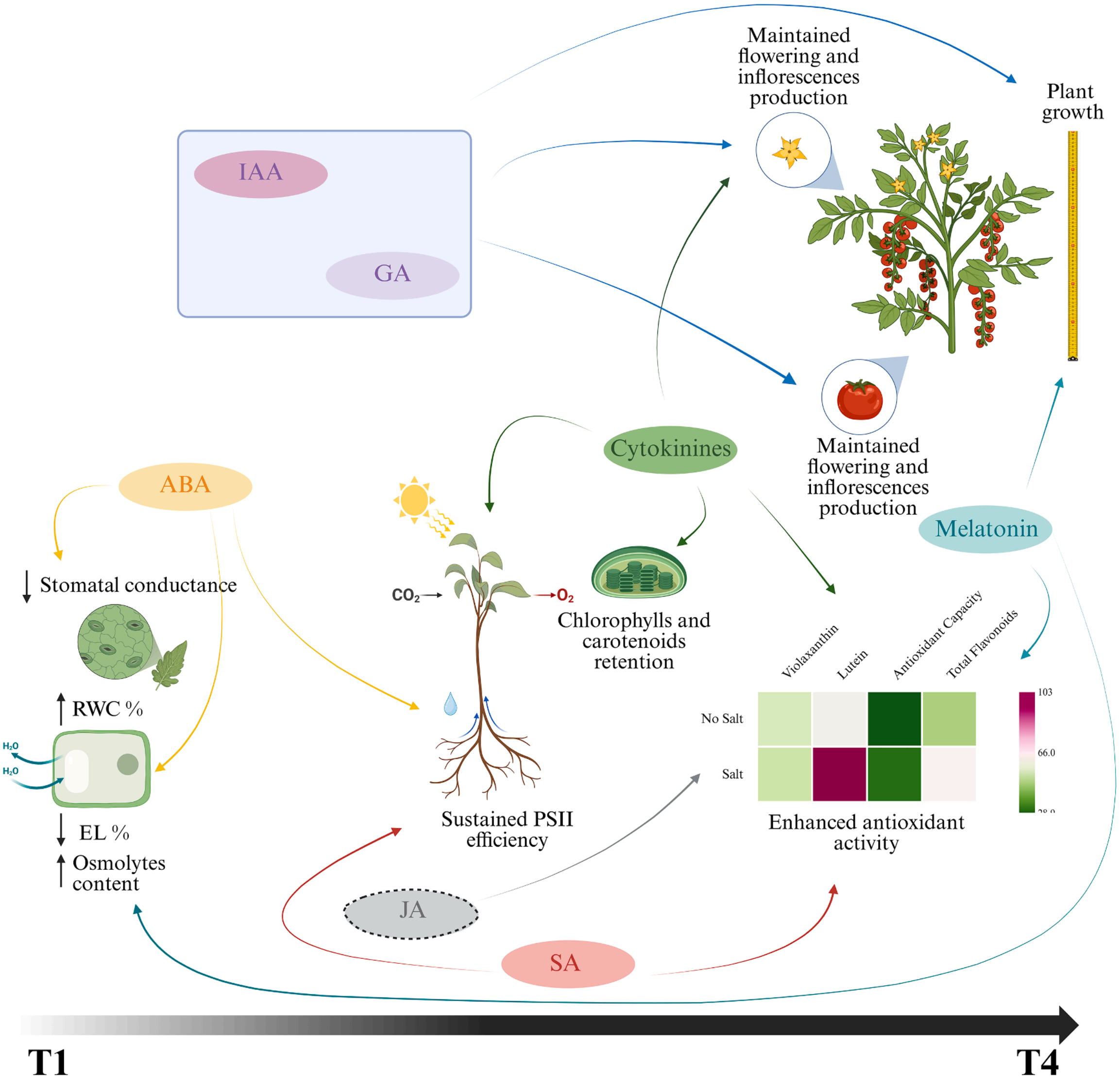


Fig. 8. Schematic representation of hormonal coordination in *Solanum pimpinellifolium* during the experiment. The arrows indicate modulation or activation of endogenous hormone levels and the associated promotion of specific physiological or developmental processes.

consistent with previous reports indicating that JA typically acts as a short-lived stress signal, showing transient accumulation during the initial phase of abiotic stress before returning to basal levels to trigger downstream protective responses, rather than representing a sustained hormonal adjustment (Muñoz-Espinoza et al., 2015). Functionally, both genetic and physiological evidence demonstrated that JA contributed to salt tolerance primarily by activating antioxidant defences and counteracting reactive oxygen species (ROS) accumulation (Ahmad et al., 2018).

In summary, hormonal regulation emerged as a unifying component linking morphological, physiological, and biochemical resilience in *S. pimpinellifolium* L.. The coordinated and timely interplay of ABA, cytokinins, auxin, gibberellins, melatonin, SA, and JA appeared to balance stress protection with the sustained maintenance of photosynthetic performance and reproductive development. A schematic representation of the hormonal coordination proposed for *S. pimpinellifolium* is described in Fig. 8. In contrast, *S. lycopersicum* L. exhibited weaker and less synchronised hormonal adjustments, which may have limited its capacity to achieve similar resilience, suggesting that the superior salt tolerance of the wild species relies on a more integrated and temporally coordinated hormonal network.

The consistency between our previous *in vitro* studies (Cialli et al., 2024; Cialli et al., 2025) and the present *in vivo* findings confirms the robustness of the selection strategy adopted in this work. The WR2 accession, which had the highest salt tolerance under controlled *in vitro* conditions (Cialli et al., 2025), also maintained superior growth, biomass accumulation, and reproductive stability in the greenhouse. This coherence across independent experiments indicates that WR2's tolerance is not an artefact of experimental conditions but rather a stable, genotype-dependent trait (Foolad, 2004). Such validation supports its use as a reliable model for detailed physiological and hormonal investigations, demonstrating the effectiveness of multi-step screening approaches in identifying truly salt-tolerant genotypes.

Finally, the use of 35 % synthetic seawater in a closed-loop hydroponic system provides a proof of concept to explore plant responses to seawater-derived salinity under controlled conditions. While not an agronomic recommendation, this approach supports research on circular water management and highlights the need for future validation under graded salinity levels and across genotypes (Tomlin et al., 2025).

5. Conclusions

This study integrated morphological, physiological and yield-related traits with detailed hormonal profiling to investigate the physiological processes underlying salt stress responses in *S. pimpinellifolium* L. and *S. lycopersicum* L. The wild species mounted a more temporally coordinated response, combining the activation of protective pathways with sustained support for photosynthesis and reproduction, thereby achieving superior tolerance compared with the cultivated tomato. Hormonal regulation emerged as major physiological component linking adaptive traits and this work provides the first physiological comprehensive evidence that *S. pimpinellifolium* relies on a synchronised network of ABA, cytokinins, auxins, gibberellins, melatonin, salicylic acid and jasmonic acid to sustain its resilience under salinity. The consistent performance of WR2 across *in vitro* and *in vivo* screenings confirm its stable, genotype-dependent salt tolerance and validates the multi-step selection strategy used in this work. The experiment, conducted in a greenhouse system closely resembling commercial closed-loop rockwool cultivation, provided insights under conditions relevant to horticultural practice that could be deepen in future works. In particular, the use of 35 % synthetic seawater in a closed-loop hydroponic system represents a proof of concept to explore plant adaptation to seawater-derived salinity under controlled conditions. Future work should expand this framework through transcriptomic and metabolomic analyses to disentangle the genetic and metabolic coordination underlying these multi-level responses.

CRediT authorship contribution statement

Giulia Carmassi: Investigation, Formal analysis. **Cialli Susanna:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luca Incrocci:** Writing – review & editing. **Antonio Ferrante:** Writing – review & editing. **Stefano Brizzolara:** Investigation, Formal analysis. **Rita Maggini:** Investigation, Formal analysis. **Alice Trivellini:** Writing – original draft, Methodology, Conceptualization. **Anna Mensuali:** Writing – original draft, Supervision, Funding acquisition, Conceptualization.

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Declaration of Competing Interest

The authors declare no conflict of interest. All authors read and approved the manuscript.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2025.106296.

Data availability

All primary data to support the findings of this study are available in "Zenodo" at DOI https://doi.org/10.5281/zenodo.17076960.

References

Agius, C., von Tucher, S., Rozhon, W., 2022. The effect of salinity on fruit quality and yield of cherry tomatoes. Horticulturae 8 (1), 59. https://doi.org/10.3390/horticulturae8010059.

Ahmad, P., Abass Ahanger, M., Nasser Alyemeni, M., Wijaya, L., Alam, P., Ashraf, M., 2018. Mitigation of sodium chloride toxicity in *Solanum lycopersicum* L. by supplementation of jasmonic acid and nitric oxide. J. Plant Interact. 13 (1), 64–72. https://doi.org/10.1080/17429145.2017.1420830.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84 (2), 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2.

Anjum, N.A., Thangavel, P., Rasheed, F., Masood, A., Pirasteh-Anosheh, H., Khan, N.A., 2023. Osmolytes: efficient oxidative stress-busters in plants. Glob. Clim. Change Plant Stress Manag. 399–409. https://doi.org/10.1002/9781119858553.ch27.

Apse, M.P., Aharon, G.S., Snedden, W.A., Blumwald, E., 1999. Salt tolerance conferred by overexpression of a vacuolar Na+/H+ antiport in Arabidopsis. Science 285 (5431), 1256–1258. https://doi.org/10.1126/science.285.5431.1256.

Asins, M.J., Bolarín, M.C., Pérez-Alfocea, F., Estañ, M.T., Martínez-Andújar, C., Albacete, A., Carbonell, E.A., 2010. Genetic analysis of physiological components of salt tolerance conferred by Solanum rootstocks. What is the rootstock doing for the scion? Theor. Appl. Genet. 121 (1), 105. https://doi.org/10.1007/s00122-010-1294-9.

Cardoso, E.F., Lopes, A.R., Dotto, M., Pirola, K., Giarola, C.M., 2021. Phenological growth stages of Gaúcho tomato based on the BBCH scale. Comun. Sci. 12. https://doi.org/10.14295/cs.v12.3490.

Carmassi, G., Bacci, L., Bronzini, M., Incrocci, L., Maggini, R., Bellocchi, G., Pardossi, A., 2013. Modelling transpiration of greenhouse gerbera (Gerbera jamesonii H. Bolus) grown in substrate with saline water in a Mediterranean climate. Sci. Hortic. 156, 9–18. https://doi.org/10.1016/j.scienta.2013.03.023.

Carmassi, G., Cialli, S., Cela, F., Romero, E.B., Gallardo, M., Incrocci, L., 2025. Use of the VegSyst v3 model to simulate seasonal dry matter production, uptake of nutrients, and evapotranspiration in a greenhouse soilless tomato crop in Tuscany. Agric. Water Manag. 314, 109508. https://doi.org/10.1016/j.agwat.2025.109508.

Cela, F., Carmassi, G., Najar, B., Taglieri, I., Sanmartin, C., Cialli, S., Incrocci, L., 2024. Salinity impact on yield, quality and sensory profile of 'Pisanello'Tuscan local tomato (Solanum lycopersicum L.) in closed soilless cultivation. Horticulturae 10 (6), 570. https://doi.org/10.3390/horticulturae10060570.

Chen, Q., Arnao, M.B., 2022. Phytomelatonin: an emerging new hormone in plants. J. Exp. Bot. 73 (17), 5773–5778. https://doi.org/10.1093/jxb/erac307.

Cialli, S., Trivellini, A., Carmassi, G., Incrocci, L., Mensuali, A., 2024. Enhancing Agrobiodiversity: Designing an In Vitro Screening Protocol for *Solanum lycopersicum* L. and *Solanum pimpinellifolium L.* L. to Explore Responses to Salinity Stress. Horticulturae 10 (4), 322. https://doi.org/10.3390/horticulturae10040322.

Cialli, S., Trivellini, A., Carmassi, G., et al., 2025. Identifying salt-tolerant traits in *Solanum pimpinellifolium* through in vitro screening to enhance crop resilience. Plant Cell Tiss. Organ Cult. 163, 55. https://doi.org/10.1007/s11240-025-03183-3Cialli.

Colebrook, E.H., Thomas, S.G., Phillips, A.L., Hedden, P., 2014. The role of gibberellin signalling in plant responses to abiotic stress. J. Exp. Biol. 217 (1), 67–75. https://doi.org/10.1242/jeb.089938.

Dobránszki, J., Mendler-Drienyovszki, N., 2014. Cytokinin-induced changes in the chlorophyll content and fluorescence of in vitro apple leaves. J. Plant Physiol. 171 (16), 1472–1478. https://doi.org/10.1016/j.jplph.2014.06.015.

El-Esawi, M.A., Elansary, H.O., El-Shanhorey, N.A., Abdel-Hamid, A.M., Ali, H.M., Elshikh, M.S., 2017. Salicylic acid-regulated antioxidant mechanisms and gene expression enhance rosemary performance under saline conditions. Front. Physiol. 8, 716. https://doi.org/10.3389/fphys.2017.00716.

Eynizadeh, P., Ravari, S.Z., Moradi, M., Dehghani, A., Dehghani, H., 2023. Determining tolerant tomato genotypes to salt stress according to physiological and morphological manner. AoB Plants 15 (6), plad037. https://doi.org/10.1093/aobpla/plad037.

Fahad, S., Hussain, S., Matloob, A., Khan, F.A., Khaliq, A., Saud, S., Huang, J., 2015. Phytohormones and plant responses to salinity stress: a review. Plant Growth Regul. 75 (2), 391–404. https://doi.org/10.1007/s10725-014-0013-y.

FAO, 2024. Global status of salt-affected soils – Main report. Rome10.4060/cd3044en.

Ferreira, C.S., Seifollahi-Aghmiuni, S., Destouni, G., Ghajarnia, N., Kalantari, Z., 2022. Soil degradation in the European mediterranean region: processes, status and consequences. Sci. Total Environ. 805, 150106. https://doi.org/10.1016/j.scitotenv.2021.150106.

Fidalgo-Illesca, C., Francini, A., Raffaelli, A., Sebastiani, L., 2025. Silicon priming triggers differential physiological, ionomic and metabolic responses in olive (Olea europaea L.) cultivars with different tolerance to salinity. Plant Physiol. Biochem., 109809 https://doi.org/10.1016/j.plaphy.2025.109809.

Foolad, M.R., 2004. Recent advances in genetics of salt tolerance in tomato. Plant Cell Tissue Organ Cult. 76 (2), 101–119.

Franzoni, G., Cocetta, G., Ferrante, A., 2021. Effect of glutamic acid foliar applications on lettuce under water stress. Physiol. Mol. Biol. Plants 27, 1059–1072. https://doi.org/10.1007/s12298-021-00984-6.

Ghanem, M.E., Albacete, A., Martínez-Andújar, C., Acosta, M., Romero-Aranda, R., Dodd, I.C., Pérez-Alfocea, F., 2008. Hormonal changes during salinity-induced leaf senescence in tomato (Solanum lycopersicum L.). J. Exp. Bot. 59 (11), 3039–3050. https://doi.org/10.1093/jxb/ern153.

Ghanem, M.E., Albacete, A., Smigocki, A.C., Frebort, I., Pospíšilová, H., Martínez-Andújar, C., Perez-Alfocea, F., 2011. Root-synthesized cytokinins improve shoot growth and fruit yield in salinized tomato (Solanum lycopersicum L.) plants. J. Exp. Bot. 62 (1), 125–140. https://doi.org/10.1093/jxb/erq266.

Ghirardelli, A., Straffelini, E., Park, E., D'Agostino, V., Masin, R., Tarolli, P., 2024. Global impact of seawater intrusion on coastal agriculture. Environ. Res. Lett. 20 (1), 013005. https://doi.org/10.1088/1748-9326/ad9bcd.

Gomiero, T., 2016. Soil degradation, land scarcity and food security: reviewing a complex challenge. Sustainability 8 (3), 281. https://doi.org/10.3390/su8030281.

Gonzales, C.F., Kelley, D.R., 2025. Interplay between auxin and abiotic stresses in maize. J. Exp. Bot. 76 (7), 1879–1887. https://doi.org/10.1093/jxb/eraf079.

Gramazio, P., Pereira-Dias, L., Vilanova, S., Prohens, J., Soler, S., Esteras, J., Díez, M.J., 2020. Morphoagronomic characterization and whole-genome resequencing of eight highly diverse wild and weedy S. pimpinellifolium and S. lycopersicum var. cerasiforme accessions used for the first interspecific tomato MAGIC population. Hortic. Res. 7. https://doi.org/10.1038/s41438-020-00395-w.

Gulzar, R.M.A., Munir, R., Yi, Z.R., et al., 2025. Genome-wide identification of *NHX* gene family and effects of salicylic acid in regulating antioxidant activity as well as nutrients deposition under salt stress in three *Brassica* species. BMC Plant Biol. 25, 740. https://doi.org/10.1186/s12870-025-06759-5.

Guo, M., Wang, X.S., Guo, H.D., Bai, S.Y., Khan, A., Wang, X.M., Li, J.S., 2022. Tomato salt tolerance mechanisms and their potential applications for fighting salinity: a review. Front. Plant Sci. 13, 949541. https://doi.org/10.3389/fpls.2022.949541.

Hadi, M.R., Karimi, N., 2012. The role of calcium in plants'salt tolerance. J. Plant Nutr. 35 (13), 2037–2054. https://doi.org/10.1093/aob/mcg058.

Hassani, A., Azapagic, A., Shokri, N., 2021. Global predictions of primary soil salinization under changing climate in the 21st century. Nat. Commun. 12 (1), 6663. https://doi.org/10.1038/s41467-021-26907-3.

Hedrich, R., Shabala, S., 2018. Stomata in a saline world. Curr. Opin. Plant Biol. 46, 87–95. https://doi.org/10.1016/j.pbi.2018.07.015.

Hniličková, H., HNILIČK, F., Orsák, M., Hejnák, V., 2019. Effect of salt stress on growth, electrolyte leakage, Na+ and K+ content in selected plant species. Plant Soil Environ. 65 (2). https://doi.org/10.17221/620/2018-PSE.

Holsteens, K., De Jaegere, I., Wynants, A., Prinsen, E.L., Van de Poel, B., 2022. Mild and severe salt stress responses are age-dependently regulated by abscisic acid in tomato. Front. Plant Sci. 13, 982622. https://doi.org/10.3389/fpls.2022.982622.

Hsieh, T.H., Li, C.W., Su, R.C., Cheng, C.P., Sanjaya, Tsai, Y.C., Chan, M.T., 2010. A tomato bZIP transcription factor, SlAREB, is involved in water deficit and salt stress response. Planta 231 (6), 1459–1473. https://doi.org/10.1007/s00425-010-1147-4.

Hudeček, M., Nožková, V., Plíhalová, L., Plíhal, O., 2023. Plant hormone cytokinin at the crossroads of stress priming and control of photosynthesis. Front. Plant Sci. 13, 1103088. https://doi.org/10.3389/fpls.2022.1103088.

Hussain, S., Hafeez, M.B., Azam, R., Mehmood, K., Aziz, M., Ercisli, S., Ren, X., 2024. Deciphering the role of phytohormones and osmolytes in plant tolerance against salt stress: implications, possible cross-talk, and prospects. J. Plant Growth Regul. 43 (1), 38–59. https://doi.org/10.1007/s00344-023-11070-4.

Hussain, T., Asrar, H., Zhang, W., Liu, X., 2023. The combination of salt and drought benefits selective ion absorption and nutrient use efficiency of halophyte Panicum antidotale. Front. Plant Sci. 14, 1091292. https://doi.org/10.3389/fpls.2023.1091292.

Javeed, H.M.R., Wang, X., Ali, M., Nawaz, F., Qamar, R., Rehman, A.U., Ismail, I.A., 2021. Potential utilization of diluted seawater for the cultivation of some summer vegetable crops: physiological and nutritional implications. Agronomy 11 (9), 1826. https://doi.org/10.3390/agronomy11091826.

Karimi, M.R., Sabokdast, M., Korang Beheshti, H., Abbasi, A.R., Bihamta, M.R., 2025. Seed priming with salicylic acid enhances salt stress tolerance by boosting antioxidant defense in Phaseolus vulgaris genotypes. BMC Plant Biol. 25 (1), 489. https://doi.org/10.1186/s12870-025-06376-2.

Kim, D.O., Chun, O.K., Kim, Y.J., Moon, H.Y., Lee, C.Y., 2003. Quantification of polyphenolics and their antioxidant capacity in fresh plums. J. Agric. Food Chem. 51 (22), 6509–6515. https://doi.org/10.1021/jf0343074.

Kindt, R., Coe, R., 2005. Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agrofor. Cent.

Kurepa, J., Shull, T.E., Smalle, J.A., 2023. Friends in arms: Flavonoids and the auxin/cytokinin balance in terrestrialization. Plants 12 (3), 517. https://doi.org/10.3390/plants12030517.

Lee, S.Y., Damodaran, P.N., Roh, K.S., 2014. Influence of salicylic acid on rubisco and rubisco activase in tobacco plant grown under sodium chloride in vitro. Saudi J. Biol. Sci. 21 (5), 417–426. https://doi.org/10.1016/j.sjbs.2014.04.002.

Li, C.Y., He, R., Tian, C.Y., Song, J., 2023a. Utilization of halophytes in saline agriculture and restoration of contaminated salinized soils from genes to ecosystem: Suaeda salsa as an example. Mar. Pollut. Bull. 197, 115728. https://doi.org/10.1016/j.marpolbul.2023.115728.

Li, N., He, Q., Wang, J., Wang, B., Zhao, J., Huang, S., Yang, T., Tang, Y., Yang, S., Aisimutuola, P., Xu, R., Hu, J., Jia, C., Ma, K., Li, Z., Jiang, F., Gao, J., Lan, H., Zhou, Y., Yu, Q., 2023b. Super-pangenome analyses highlight genomic diversity and structural variation across wild and cultivated tomato species. Nat. Genet. 55 (5), 852–860. https://doi.org/10.1038/s41588-023-01340-y.

Liang, K., Chen, Y., Hou, J., Yan, F., Liu, F., 2024. ABA-mediated stomatal response modulates the effects of drought, salinity and combined stress on tomato plants grown under elevated CO2. Environ. Exp. Bot. 223, 105797. https://doi.org/10.1016/j.envexpbot.2024.105797.

Liu, D.D., Sun, X.S., Liu, L., Shi, H.D., Chen, S.Y., Zhao, D.K., 2019. Overexpression of the melatonin synthesis-related gene SlCOMT1 improves the resistance of tomato to salt stress. Molecules 24 (8), 1514. https://doi.org/10.3390/molecules24081514.

Liu, J., Shabala, S., Zhang, J., Ma, G., Chen, D., Shabala, L., Zhao, Q., 2020. Melatonin improves rice salinity stress tolerance by NADPH oxidase-dependent control of the plasma membrane K+ transporters and K+ homeostasis. Plant Cell Environ. 43 (11), 2591–2605. https://doi.org/10.1111/pce.13759.

Maggini, R., Benvenuti, S., Leoni, F., Pardossi, A., 2018. Terracrepolo (Reichardia picroides (L.) Roth.): wild food or new horticultural crop? Sci. Hortic. 240, 224–231. https://doi.org/10.1016/j.scienta.2018.06.018.

Maggini, R., Benvenuti, S., Leoni, F., Incrocci, L., Pardossi, A., 2021. Effects of NaCl on hydroponic cultivation of Reichardia picroides (L.) Roth. Agronomy 11 (11), 2352. https://doi.org/10.3390/agronomy11112352.

Maggio, A., Raimondi, G., Martino, A., De Pascale, S., 2007. Salt stress response in tomato beyond the salinity tolerance threshold. Environ. Exp. Bot. 59 (3), 276–282. https://doi.org/10.1016/j.envexpbot.2006.02.002.

Martinez, J.P., Antunez, A., Pertuze, R., ACOSTA, M.D.P., Palma, X., Fuentes, L., Lutts, S., 2012. Effects of saline water on water status, yield and fruit quality of wild (Solanum chilense) and domesticated (Solanum lycopersicum var. cerasiforme) tomatoes. Exp. Agric. 48 (4), 573–586. https://doi.org/10.1017/S001447971200066X.

Martínez-Andújar, C., Martínez-Pérez, A., Albacete, A., Martínez-Melgarejo, P.A., Dodd, I.C., Thompson, A.J., Pérez-Alfocea, F., 2021. Overproduction of ABA in rootstocks alleviates salinity stress in tomato shoots. Plant Cell Environ. 44 (9), 2966–2986. https://doi.org/10.1111/pce.14121.

Martínez-Cuenca, M.R., Pereira-Dias, L., Soler, S., López-Serrano, L., Alonso, D., Calatayud, Á., Díez, M.J., 2020. Adaptation to water and salt stresses of Solanum pimpinellifolium L. and Solanum lycopersicum var. cerasiforme. Agronomy 10 (8), 1169. https://doi.org/10.3390/agronomy10081169.

Massaretto, I.L., Albaladejo, I., Purgatto, E., Flores, F.B., Plasencia, F., Egea-Fernández, J. M., Egea, I., 2018. Recovering tomato landraces to simultaneously improve fruit yield and nutritional quality against salt stress. Front. Plant Sci. 9, 1778. https://doi.org/10.3389/fpls.2018.01778.

Meucci, A., Ghelardi, C., Maggini, R., Malorgio, F., Pezzarossa, B., Rosellini, I., Mensuali, A., 2024. Insights into orris (Iris pallida Lam.) in vivo acclimatization and response to salt stress via exogenous melatonin application. Agriculture 14 (12), 2353. https://doi.org/10.3390/agriculture14122353.

Monforte, A.J., 2020. Time to exploit phenotypic plasticity. J. Exp. Bot. 71 (18), 5295–5297.

Morton, M., Fiene, G., Ahmed, H.I., Rey, E., Abrouk, M., Angel, Y., Julkowska, M.M., 2024. Deciphering salt stress responses in Solanum pimpinellifolium L. through high-throughput phenotyping. Plant J. 119 (5), 2514–2537. https://doi.org/10.1111/tpj.16894.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59 (1), 651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911.

Muñoz-Espinoza, V.A., López-Climent, M.F., Casaretto, J.A., Gómez-Cadenas, A., 2015. Water stress responses of tomato mutants impaired in hormone biosynthesis reveal abscisic acid, jasmonic acid and salicylic acid interactions. Front. Plant Sci. 6, 997. https://doi.org/10.3389/fpls.2015.00997.

Mutasa-Göttgens, E., Hedden, P., 2009. Gibberellin as a factor in floral regulatory networks. J. Exp. Bot. 60 (7), 1979–1989. https://doi.org/10.1093/jxb/erp040.

Nali, C., Paoletti, E., Marabottini, R., Della Rocca, G., Lorenzini, G., Paolacci, A.R., Badiani, M., 2004. Ecophysiological and biochemical strategies of response to ozone in Mediterranean evergreen broadleaf species. Atmos. Environ. 38 (15), 2247–2257. https://doi.org/10.1016/j.atmosenv.2003.11.043.

Nikalje, G.C., Srivastava, A.K., Pandey, G.K., Suprasanna, P., 2018. Halophytes in biosaline agriculture: mechanism, utilization, and value addition. Land Degrad. Dev. 29 (4), 1081–1095. https://doi.org/10.1002/ldr.2819.

Oksanen, J., 2022. vegan: community ecology packageR. Package Version246(No Title).

Pailles, Y., Awlia, M., Julkowska, M., Passone, L., Zemmouri, K., Negrão, S., Tester, M., 2020. Diverse traits contribute to salinity tolerance of wild tomato seedlings from the Galapagos Islands. Plant Physiol. 182 (1), 534–546. https://doi.org/10.1104/pp.19.00700.

Pardo-Hernández, M., García-Pérez, P., Lucini, L., Rivero, R.M., 2024. Multi-omics exploration of the involvement of ABA in identifying unique molecular markers for single and combined stresses in tomato plants. J. Exp. Bot. https://doi.org/10.1093/jxb/erae372.

Patanè, C., Cosentino, S.L., Romano, D., Toscano, S., 2022. Relative water content, proline, and antioxidant enzymes in leaves of long shelf-life tomatoes under drought stress and rewatering. Plants 11 (22), 3045. https://doi.org/10.3390/plants11223045.

Peleg, Z., Blumwald, E., 2011. Hormone balance and abiotic stress tolerance in crop plants. Curr. Opin. Plant Biol. 14 (3), 290–295. https://doi.org/10.1016/j.pbi.2011.02.001.

Rahnama, A., Poustini, K., Tavakkol-Afshari, R., Ahmadi, A., Alizadeh, H., 2011. Growth properties and ion distribution in different tissues of bread wheat genotypes (Triticum aestivum L.) differing in salt tolerance. J. Agron. Crop Sci. 197 (1), 21–30. https://doi.org/10.1111/j.1439-037X.2010.00437.x.

Rao, E.S., Kadirvel, P., Symonds, R.C., Ebert, A.W., 2013. Relationship between survival and yield related traits in Solanum pimpinellifolium L. under salt stress. Euphytica 190 (2), 215–228. https://doi.org/10.1007/s10681-012-0801-2.

Razali, R., Bougouffa, S., Morton, M.J., Lightfoot, D.J., Alam, I., Essack, M., Arold, S.T., Kamau, A.A., Schmöckel, S.M., Pailles, Y., Shahid, M., Michell, C.T., Ho, Y.S., Tester, M., Bajic, V.B., Negrão, S., 2018. The genome sequence of the wild tomato solanum pimpinellifolium l. provides insights into salinity tolerance. Front. Plant Sci. 9, 390082. https://doi.org/10.3389/fpls.2018.01402.

Roșca, M., Mihalache, G., Stoleru, V., 2023. Tomato responses to salinity stress: From morphological traits to genetic changes. Front. Plant Sci. 14, 1118383. https://doi.org/10.3389/fpls.2023.1118383.

Romeo, S., Francini, A., Ariani, A., Sebastiani, L., 2014. Phytoremediation of Zn: identify the diverging resistance, uptake and biomass production behaviours of poplar clones under high zinc stress. Water Air Soil Pollut. 225, 1813. https://doi.org/10.1007/s11270-013-1813-9.

Sah, S.K., Reddy, K.R., Li, J., 2016. Abscisic acid and abiotic stress tolerance in crop plants. Front. Plant Sci. 7, 571. https://doi.org/10.3389/fpls.2016.00571.

Salehin, M., 2024. Emerging roles of auxin in plant abiotic stress tolerance. Physiol. Plant. 176 (6), e14601. https://doi.org/10.1111/ppl.14601.

Schouten, H.J., Tikunov, Y., Verkerke, W., Finkers, R., Bovy, A., Bai, Y., Visser, R.G., 2019. Breeding has increased the diversity of cultivated tomato in the Netherlands. Front. Plant Sci. 10, 500236. https://doi.org/10.3389/fpls.2019.01606.

Serrani, J.C., Sanjuán, R., Ruiz-Rivero, O., Fos, M., García-Martínez, J.L., 2007. Gibberellin regulation of fruit set and growth in tomato. Plant Physiol. 145 (1), 246–257. https://doi.org/10.1104/pp.107.098335.

Siddiqui, M.H., Alamri, S., Alsubaie, Q.D., Ali, H.M., 2020. Melatonin and gibberellic acid promote growth and chlorophyll biosynthesis by regulating antioxidant and methylglyoxal detoxification system in tomato seedlings under salinity. J. Plant Growth Regul. 39 (4), 1488–1502. https://doi.org/10.1007/s00344-020-10122-3.

Singh, D., Debnath, P., Sane, A.P., Sane, V.A., 2023. Tomato (Solanum lycopersicum) WRKY23 enhances salt and osmotic stress tolerance by modulating the ethylene and auxin pathways in transgenic Arabidopsis. Plant Physiol. Biochem. 195, 330–340. https://doi.org/10.1016/j.plaphy.2023.01.002.

Singh, P., Choudhary, K.K., Chaudhary, N., Gupta, S., Sahu, M., Tejaswini, B., Sarkar, S., 2022. Salt stress resilience in plants mediated through osmolyte accumulation and its crosstalk mechanism with phytohormones. Front. Plant Sci. 13, 1006617. https://doi.org/10.3389/fpls.2022.1006617.

Soltabayeva, A., Ongaltay, A., Omondi, J.O., Srivastava, S., 2021. Morphological, physiological and molecular markers for salt-stressed plants. Plants 10 (2), 243. https://doi.org/10.3390/plants10020243.

Soma, F., Takahashi, F., Yamaguchi-Shinozaki, K., Shinozaki, K., 2021. Cellular phosphorylation signaling and gene expression in drought stress responses: ABA-dependent and ABA-independent regulatory systems. Plants 10 (4), 756. https://doi.org/10.3390/plants10040756.

Song, C., Acuña, T., Adler-Agmon, M., Rachmilevitch, S., Barak, S., Fait, A., 2022. Leveraging a graft collection to develop metabolome-based trait prediction for the selection of tomato rootstocks with enhanced salt tolerance. Hortic. Res. 9, uhac061. https://doi.org/10.1093/hr/uhac061.

Stavi, I., Thevs, N., Priori, S., 2021. Soil salinity and sodicity in drylands: a review of causes, effects, monitoring, and restoration measures. Front. Environ. Sci. 9, 712831. https://doi.org/10.3389/fenvs.2021.712831.

Strasser, R.J., Tsimilli-Michael, M., Srivastava, A., 2004. Analysis of the chlorophyll a fluorescence transient. In: *Chlorophyll a fluorescence: a signature of photosynthesis*. Springer Netherlands, Dordrecht, pp. 321–362.

Sun, F., Wang, Y., Liu, G., Fang, D., Sun, M., Bao, Z., Ma, F., 2024. Salt stress induces SFT expression to promote early flowering and inhibits floral organ development by disturbing cell cycle in tomato. Veg. Res. 4 (1). https://doi.org/10.48130/vegres-0024-0017.

Takeno, K., 2011. Stress-induced flowering. Proceeding of Abiotic stress responses in plants: Metabolism, productivity and sustainability. Springer New York, New York, NY, pp. 331–345. https://doi.org/10.1007/978-1-4614-0634-1_17.

Talla, S.K., Panigrahy, M., Kappara, S., Nirosha, P., Neelamraju, S., Ramanan, R., 2016. Cytokinin delays dark-induced senescence in rice by maintaining the chlorophyll cycle and photosynthetic complexes. J. Exp. Bot. 67 (6), 1839–1851. https://doi.org/10.1093/jxb/erv575.

Tan, D.X., Hardeland, R., Manchester, L.C., Korkmaz, A., Ma, S., Rosales-Corral, S., Reiter, R.J., 2012. Functional roles of melatonin in plants, and perspectives in nutritional and agricultural science. J. Exp. Bot. 63 (2), 577–597. https://doi.org/10.1093/jxb/err256.

Tester, M., Davenport, R., 2003. Na+ tolerance and Na+ transport in higher plants. Ann. Bot. 91 (5), 503–527.

Tian, Z., Wang, J.W., Li, J., Han, B., 2021. Designing future crops: challenges and strategies for sustainable agriculture. Plant J. 105 (5), 1165–1178. https://doi.org/10.1111/tpj.15107.

Tomlin, M., Bridges, W., Su, Q., Karthikeyan, R., Jeong, B.R., Liu, H., Adelberg, J., 2025. Combining diluted seawater and fertilizer in an ion-based multivariate approach as an effective assay of salt tolerance in brassica juncea seedlings. Horticulturae 11 (7), 820. https://doi.org/10.3390/horticulturae11070820.

Trivellini, A., Lucchesini, M., Ferrante, A., Carmassi, G., Scatena, G., Vernieri, P., Mensuali-Sodi, A., 2016. Survive or die? A molecular insight into salt-dependant signaling network. Environ. Exp. Bot. 132, 140–153. https://doi.org/10.1016/j.envexpbot.2016.07.007.

Trivellini, A., Carmassi, G., Scatena, G., Vernieri, P., Ferrante, A., 2023. Molecular and physiological responses to salt stress in salinity-sensitive and tolerant Hibiscus rosa-sinensis cultivars. Mol. Hortic. 3 (1), 28. https://doi.org/10.1186/s43897-023-00075-y.

Verma, V., Ravindran, P., Kumar, P.P., 2016. Plant hormone-mediated regulation of stress responses. BMC Plant Biol. 16 (1), 86. https://doi.org/10.1186/s12870-016-0771-y.

Wang, B., Wang, J., Yang, T., Wang, J., Dai, Q., Zhang, F., Li, N., 2023. The transcriptional regulatory network of hormones and genes under salt stress in tomato plants (Solanum lycopersicum L.). Front. Plant Sci. 14, 1115593. https://doi.org/10.3389/fpls.2023.1115593.

Wu, H., 2018. Plant salt tolerance and Na+ sensing and transport. Crop J. 6 (3), 215–225. https://doi.org/10.1016/j.cj.2018.01.003.

Yang, H., Du, T., Mao, X., Ding, R., Shukla, M.K., 2019. A comprehensive method of evaluating the impact of drought and salt stress on tomato growth and fruit quality based on EPIC growth model. Agric. Water Manag. 213, 116–127. https://doi.org/10.1016/j.agwat.2018.10.010.

Yang, Sijia, Zhao, Yuqing, Qin, Xiaolong, Ding, Chunbang, Chen, Yanger, Tang, Zizhong, Huang, Yan, Reiter, Russel J., Yuan, Shu, Yuan, Ming, 2022. New insights into the role of melatonin in photosynthesis. J. Exp. Bot. 73 (17), 5918–5927. https://doi.org/10.1093/jxb/erac230.

Yin, Y.G., Tominaga, T., Iijima, Y., Aoki, K., Shibata, D., Ashihara, H., Matsukura, C., 2010. Metabolic alterations in organic acids and γ-aminobutyric acid in developing tomato (Solanum lycopersicum L.) fruits. Plant Cell Physiol. 51 (8), 1300–1314. https://doi.org/10.1093/pcp/pcq150.

Yoshida, T., Mogami, J., Yamaguchi-Shinozaki, K., 2014b. ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. Curr. Opin. Plant Biol. 21, 133–139. https://doi.org/10.1016/j.pbi.2014.07.009.

Yoshida, T., Mogami, J., Yamaguchi-Shinozaki, K., 2014a. ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. Curr. Opin. Plant Biol. 21, 133–139. https://doi.org/10.1016/j.pbi.2014.07.009.

Yoshida, T., Mogami, J., Yamaguchi-Shinozaki, K., 2014c. ABA-dependent and ABA-independent signalling in response to osmotic stress in plants. Curr. Opin. Plant Biol. 21, 133–139. https://doi.org/10.1016/j.pbi.2014.07.009.

Young, A.J., 1991. The photoprotective role of carotenoids in higher plants. Physiol. Plant. 83 (4), 702–708. https://doi.org/10.1111/j.1399-3054.1991.tb02490.x.

Yu, Z., Duan, X., Luo, L., Dai, S., Ding, Z., Xia, G., 2020. How plant hormones mediate salt stress responses. Trends Plant Sci. 25 (11), 1117–1130. https://doi.org/10.1016/j.tplants.2020.06.008.

Yusuf, M., Saeed, T., Almenhali, H.A., Azzam, F., Hamzah, A.I.A.H., Khan, T.A., 2024. Melatonin improved efficiency of 24-epibrassinolide to counter the collective stress of drought and salt through osmoprotectant and antioxidant system in pea plants. Sci. Hortic. 323, 112453. https://doi.org/10.1016/j.scienta.2023.112453.

Zhang, H., Zhu, J., Gong, Z., Zhu, J.K., 2022a. Abiotic stress responses in plants. Nat. Rev. Genet. 23 (2), 104–119. https://doi.org/10.1038/s41576-021-00413-0.

Zhang, R., Wang, Y., Hussain, S., Yang, S., Li, R., Liu, S., Hou, H., 2022b. Study on the effect of salt stress on yield and grain quality among different rice varieties. Front. Plant Sci. 13, 918460. https://doi.org/10.3389/fpls.2022.918460.

Zhang, Y., Kaiser, E., Li, T., Marcelis, L.F., 2022c. NaCl affects photosynthetic and stomatal dynamics by osmotic effects and reduces photosynthetic capacity by ionic effects in tomato. J. Exp. Bot. 73 (11), 3637–3650. https://doi.org/10.1093/jxb/erac078.

Zhao, G., Yu, H., Liu, M., Lu, Y., Ouyang, B., 2017. Identification of salt-stress responsive microRNAs from Solanum lycopersicum and Solanum pimpinellifolium. Plant Growth Regul. 83 (1), 129–140. https://doi.org/10.1007/s10725-017-0289-9.

Zhao, S., Zhang, Q., Liu, M., Zhou, H., Ma, C., Wang, P., 2021. Regulation of plant responses to salt stress. Int. J. Mol. Sci. 22 (9), 4609. https://doi.org/10.3390/ijms22094609.

Žižková, E., Dobrev, P.I., Muhovski, Y., Hošek, P., Hoyerová, K., Haisel, D., Hichri, I., 2015. Tomato (Solanum lycopersicum L.) SlIPT3 and SlIPT4 isopentenyltransferases mediate salt stress response in tomato. BMC Plant Biol. 15 (1), 85. https://doi.org/10.1186/s12870-015-0415-7.

Zörb, Christian, Geilfus, C.-M., Dietz, K.-J., 2019. Salinity and crop yield. Plant Biol. 21, 31–38. https://doi.org/10.1111/plb.12884.

Zwack, P.J., Rashotte, A.M., 2015. Interactions between cytokinin signalling and abiotic stress responses. J. Exp. Bot. 66 (16), 4863–4871. https://doi.org/10.1093/jxb/erv172.