Horticultural Science (Prague), 52, 2025 (4): 353–362 *Original Paper*

https://doi.org/10.17221/109/2023-HORTSCI

Knowing your enemy before taking the field: A screening of salt and UV-B treatments to boost the biochemical defences of tomato (*Solanum lycopersicum* L., 'Moneymaker' cultivar) plantlets in controlled conditions

*Maria Calogera Sciampagna[1], Alessia Mannucci[1], Salvatore Limpido[1], Annamaria Ranieri[1,2], Antonella Castagna[1,2], Marco Santin[1]**

[1]Department of Agriculture, Food and Environment, University of Pisa, Pisa, Italy
[2]Interdepartmental Research Center Nutrafood "Nutraceuticals and Food for Health", University of Pisa, Pisa, Italy

**Corresponding author: marco.santin@unipi.it*

Citation: Sciampagna M.C., Mannucci A., Limpido S., Ranieri A., Castagna A., Santin M. (2025): Knowing your enemy before taking the field: A screening of salt and UV-B treatments to boost the biochemical defenses of tomato (*Solanum lycopersicum* L., 'Moneymaker' cultivar) plantlets in controlled conditions. Hort. Sci. (Prague), 52: 353–362.

Abstract: Plants are commonly exposed to different abiotic stress factors that can threaten their growth and development. Abiotic treatments might be used as a tool to increase the tolerance of plants grown in controlled environments before being transplanted in open fields, but this technique needs a careful choice of the stressor dose. We screened several UV-B radiation doses (1 h, 3 h, 6 h and 8 h per day) and NaCl doses (75 mM, 150 mM, 300 mM), separately, to be employed as preconditioning treatments of tomato plantlets (*Solanum lycopersicum* L., 'Moneymaker' cultivar) cultivated in a controlled environment. Biometric parameters and antioxidant compounds were quantified in leaves and roots. Our results showed that the application of mild abiotic treatments such as 75 mM NaCl for 14 days or 8 h/day UV-B (18.43 kJ/m^2) for 7 days to hydroponically grown tomato plantlets can increase the content of foliar total phenolics and flavonoids without inducing strong impairments in the plant growth and development. Interestingly, this work provides evidence that the UV-B radiation, although perceived only by the above-ground organs of the plants, also induces some morphological and biochemical changes in the root system.

Keywords: biometric parameters; leaves and roots; phenols; preconditioning; salt stress; ultraviolet radiation

Plants are commonly subjected to abiotic and biotic stresses that can threaten their growth and development, and therefore cause a decrease in crop yields. The negative effects of abiotic stress are nowadays worsened by climate change, which determines a higher frequency of extreme weather (Fedoroff et al. 2010; Raza et al. 2019). For these reasons, increasing plant tolerance is fundamental to coping with climate change and ensuring food security and more resilient, productive systems. Indeed, crops with weak stress tolerance require higher amounts of water and fertiliser, placing a heavy strain on the environment (Zhu 2016).

Among the main abiotic factors threatening worldwide agriculture, soil and water salinisation are a growing problem in the Mediterranean regions

---

Supported by the PhD. program of Agriculture, Food and Environment fellowship, University of Pisa, Pisa, Italy.

(Hassani et al. 2020). Salinity affects 25–30% of all irrigated land, and it is estimated that by 2050, it will affect 50% of soils (Naveed et al. 2020). The problems associated with salinisation are worsened by unsustainable agricultural practices, global climate change, particularly rising temperatures, and reduced water availability. Salinity has different effects depending on the stage of the plant growth, the degree of tolerance of the species (glycophytes or halophytes), the time of exposure to stress, and the salinity level (Acosta-Motos et al. 2017). A typical morphological response to salt stress is a reduction in the development of both the aerial part and the roots (Acosta-Motos et al. 2017). High levels of salts induce osmotic effects, reducing the water uptake by roots (physiological drought), and the excess of ion uptake produces cytotoxicity and pH/nutrient imbalance, interfering with physiological and cellular processes (Negrão et al. 2017; Hamidi-Moghaddam et al. 2019). Further, this stressor can trigger metabolic activities that promote the overproduction of reactive oxygen species (ROS), thereby promoting protein denaturation, lipid peroxidation, and nucleotide degradation, and, consequently, causing cellular damage and, ultimately, cell death (Nadeem et al. 2022). The damaging effects of ROS in plants can be prevented, reduced or eliminated by enzymatic and non-enzymatic defence systems (Ferreira-Silva et al. 2012), among which are phenolic compounds and flavonoids. These latter have a recognised role not only in the responses to biotic and abiotic stresses, but also as modulators of plant growth (Daryanavard et al. 2023). Accordingly, treatments for seeds and seedlings that increase their content may boost plant development and resilience after transplant. Light is an essential environmental factor for plant growth and development. UV radiation, specifically the UV-B region (280–315 nm), is a significant environmental factor influencing plant morphology and physiology (Robson et al. 2015). Nowadays, UV-B is recognised as an essential component of the natural light environment that, depending on the wavelength, intensity, and duration of exposure, results in the activation of specific signalling pathways and downstream gene expression, or in an unspecific stress response (Crestani et al. 2023). The specific UVR8 signalling route promotes photomorphogenetic changes, including alterations in leaf shape and width, decreased stem elongation, root growth, and the induction of cotyledon expansion (Robson et al. 2015). By interacting and (partially) overlapping with other signal transduction pathways originating from different abiotic and biotic stimuli, and modifying the partitioning of resources to plant growth or defense, low UV-B dose ultimately can provide positive effects as the induction of metabolites biosynthesis able to increase the plant tolerance and resistance to other stressors (Brown et al. 2005; Dhanya Thomas, Puthur 2017; Mannucci et al. 2020; Meyer et al. 2021; Santin et al. 2022). The well-known stimulation of phenolic and flavonoid biosynthesis (Clayton et al. 2018; Santin et al. 2021) by UV-B has been related to the defence against *Botrytis cinerea* in *Arabidopsis* by Demkura and Ballare (2012), who attributed this achievement to a syringyl-type lignin. Similarly, priming of lettuce (*Lactuca sativa*) with UV-B led to increased accumulation of phenolic compounds, in particular quercetin flavonoids, that significantly correlated with the reduced severity of downy mildew disease caused by *Bremia lactucae* (McLay et al. 2020). UV-B priming of rice (*Oryza sativa* L.) seeds and seedlings has been proven effective in conferring cross tolerance also towards abiotic stresses, such as NaCl (Dhanya Thomas et al. 2020).

In this scenario, abiotic treatments can increase the tolerance of seedlings produced in controlled conditions before transplanting in open fields where plants could likely face multiple stressors. However, this technique needs a careful choice of the stressor dose, which must also rely on the species/varieties taken into account. The objective of the present research was to check suitable UV-B radiation and NaCl doses to be employed as a treatment of tomato seedlings (*Solanum lycopersicum* L., 'Moneymaker' cultivar) cultivated in a controlled environment and to understand how these kinds of abiotic treatments alter the plant morphological characteristics, polyphenol content and antioxidant activity, at both foliar and root levels. These modifications might represent some fundamental preconditions for a better performance once transplanted in stressful environments.

MATERIAL AND METHODS

Plant material and growth conditions

Tomato seeds (*Solanum lycopersicum* L., 'Moneymaker' cultivar) were sterilised in 5% sodium hypochlorite for 20 min under magnetic stirring and germinated on water-soaked paper. Seedlings were moved in perlite-containing pots and moistened regularly with half-strength Hoagland nutri-

https://doi.org/10.17221/109/2023-HORTSCI

ent solution. The Hoagland solution was prepared as follows: N-NO_3 7.5 mM, P-H_2PO_4 0.5 mM, K 3.0 mM, Ca 2.5 mM, Mg 1.0 mM, Fe 25.0 µM, B 23.1 mM, Mn 4.6 mM, Zn 0.39 mM, Cu 0.16 mM, Mo 0.06 mM in Milli-Q water. The pH of the solution was 5.56, and the electrical conductivity (EC) was 1.15 mS/cm. Seven days after sowing, the substrate was gently washed away from the roots and seedling were transferred to a hydroponic system in a climatic chamber (24 °C, 85% relative humidity) with a 16 h light/8 h dark photoperiod and photosynthetic photon flux density (PPFD) of 228 µmol/m^2/s supplied by blue/red (1 : 2 ratio) and green (10%) light-emitting diodes (LEDs) (C-LED, Imola, Italy). The Hoagland solution was completely replaced weekly. 24-day-old tomato plantlets were subjected to either a UV-B or NaCl treatment, respectively ($n = 20$ for each treatment).

NaCl treatments. Three different NaCl (Sigma-Aldrich Chemical Co., St. Louis, MO, USA), concentrations within the Hoagland solution were tested: 0 mM (control), 75 mM, 150 mM, and 300 mM. These concentrations were selected based on the scientific literature related to tomato plants (Roșca et al. 2023). During the experiment, the solutions were completely replaced once a week. Tomato plants were evaluated and sampled after 14 days from the beginning of the treatment.

UV-B treatments. The UV-B irradiation was provided by UV-B LEDs (C-LED, Imola, Italy; 0.64 W/m^2 at plant height, 310 ± 15 nm emission peak). The Tropospheric Emissions Monitoring Internet Service (TEMIS) database (www.temis.nl/uvradiation/UVdose.html) (version 2.0; accessed Apr 3, 2024) reports that the highest UV index recorded at Rome (Italy) in the summer of 2023 was 10.493, corresponding to 0.26 W/m^2.

Five daily UV-B exposures were tested: 0 h (control), 1 h (2.30 kJ/m^2), 3 h (6.91 kJ/m^2), 6 h (13.82 kJ/m^2), 8 h (18.43 kJ/m^2). The spectral irradiance was determined with the spectrometer (FLAME-T-XR1-ES S/N: FLMT07829, Ocean Insight, Germany) with fibre optics (QP400-1-UV-BX; Ocean Insight, Germany) and cosine corrector (CC-3-UV-S; Ocean Insight, Germany). Tomato plants were evaluated and sampled 7 days after the beginning of the UV-B irradiation.

Measurement of biometric parameters

Ten individual plants (biological replicates) were used for each group to measure stem and root length, total leaf number per plant and total leaf area (cm^2). Stem length, defined as the distance from the base to the vegetative shoot apex, and root length, representing the main root's extent for each plant, were assessed using a ruler. The total leaf area was calculated using Easy Leaf Area software version 2.0 (Easlon, Bloom 2014).

Extraction and quantification of total phenolics, flavonoids and antioxidant activity

The biochemical analyses on leaves and roots (3 biological replicates, each representing a pool of 3 plants) were performed on samples collected and immediately frozen in liquid nitrogen and stored at –80 °C before being freeze-dried. Extraction was conducted in 80% methanol on freeze-dried material following the procedure described by Tavarini et al. (2019).

Concentration of total phenolic compounds was determined using the Folin-Ciocalteau method (Borbalàn et al. 2003) and expressed as mg of gallic acid equivalents per g of fresh weight (mg GAE/g FW).

Flavonoid content was determined as described by Kim et al. (2003) and reported as mg of catechin equivalents (mg CE/g FW).

The antioxidant activity of the phenolic extracts was determined using the ABTS [2,2'-azinobis (3-ethylbenzothiazoline-6-sulphonic acid)] assay (Re et al. 1999) by reading the absorbance at 734 nm and reporting the results as µmol of Trolox equivalent antioxidant capacity (µmol TEAC/g FW).

Total phenolic and flavonoid concentrations and antioxidant capacity were quantified using standard curves of the respective commercial standards (Sigma-Aldrich Chemical Co., St. Louis, MO, USA). An Ultrospec 2100 pro-UV-vis spectrophotometer (Amersham Biosciences, UK) was used for all the spectrophotometric assays conducted.

Statistical analysis

Differences among UV-B- and NaCl-treated groups were evaluated separately by one-way ANOVA followed by post hoc Tukey-Kramer test ($P < 0.05$) using JMP software version 18.0 (SAS Institute, Inc., Cary, NC, USA). Data are expressed as mean ± standard error (SE).

RESULTS

Effect of salinity treatments on plant morphological parameters, phenolic compounds, flavonoids, and antioxidant activity

Figure 1 shows the tomato plantlets grown at different NaCl concentrations. The 300 mM NaCl solu-

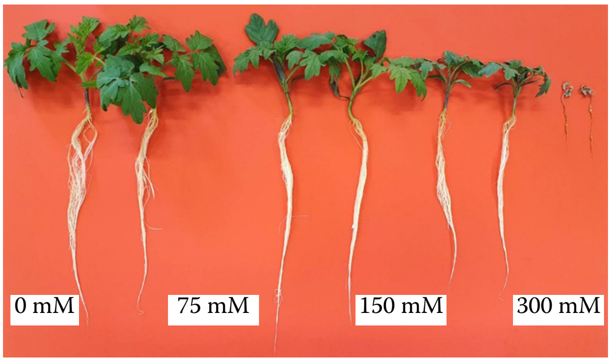

Figure 1. Effect of increasing NaCl treatments (0 mM, 75 mM, 150 mM, 300 mM) on the growth of tomato plants

tion caused a marked growth inhibition and resulted in early plant death; therefore, it was not considered in the further analyses.

The biometric data under the different NaCl concentrations are reported in Table 1. The plant growth varied according to the different salt concentrations. In particular, the treatment with 300 mM NaCl greatly damaged the leaves, causing yellowing and arrested growth. Concerning the aerial part, 75 mM and 150 mM NaCl reduced the leaf area by 29% and 68%, respectively. Leaf number, leaf FW and stem length did not differ between 0 and 75 mM, while a negative effect was caused by 150 mM concentration with respect to both control (–38%, –53% and –31%, respectively) and 75 mM (–33%, –44% and –25%, respectively).

Root length was reduced only by the 150 mM NaCl treatment (–31 % and –16 %, with respect to control and 75 mM, respectively), while root FW was different between the two NaCl treatments, with a –33% in 150mM with respect to 75mM.

Finally, the total fresh biomass (aerial part and roots, AP + R) of the 150 mM-treated plants was 48% and 41% lower than the 0 mM- and the 75 mM-treated plants, respectively, while shoot/root length was unaffected by the treatment.

Total phenols and flavonoids contents (Figure 2) were quantified in leaves and roots of control and NaCl-treated plants. Total phenols concentration in roots progressively decreased as salinity increased (–28% for 75 mM and –45% for 150 mM with respect to control plants) (Figure 2A), while this trend was not observed in leaves. The concentration of leaf flavonoids (Figure 2B) increased by 55% and 80% when plants were treated with 75 mM and 150 mM NaCl, respectively. Also, the leaf antioxidant activity (Figure 2C) registered an increase under salinity conditions (+43% for 75 mM and +57% for 150 mM). However, no significant differences were observed in root flavonoid concentration and antioxidant activity.

Effect of UV-B treatments on plant morphological parameters, phenolic compounds, flavonoids, and antioxidant activity

The biometric parameters were less influenced by the different UV-B daily doses than by salinity (Table 2). Considering the morphological parameters investigated in the aerial part of the plants, the number of leaves was negatively affected only by the 8 h UV-B treatment, where the treated plants displayed a 30% reduction compared to the control, 1 h and 3 h UV-B-treated plants, and a 26% re-

Table 1. Biometric parameters in untreated (0 mM) and NaCl-treated tomato plants (75 mM and 150 mM) for 14 days

		NaCl treatment			
		0 mM	75 mM	150 mM	*P*
Aerial part (AP)	leaf area (cm^2)	17.3 ± 1.3^{a}	12.2 ± 2.0^{b}	5.4 ± 0.5^{c}	0.0001
	leaves (number)	3.6 ± 0.2^{a}	3.3 ± 0.3^{a}	2.2 ± 0.1^{b}	< 0.0001
	leaf fresh weight (g)	3.0 ± 0.2^{a}	2.5 ± 0.4^{a}	1.4 ± 0.1^{b}	0.0008
	stem length (cm)	3.8 ± 0.2^{a}	3.5 ± 0.1^{a}	2.6 ± 0.1^{b}	< 0.0001
Roots (R)	fresh weight (g)	0.8 ± 0.1^{ab}	0.9 ± 0.1^{a}	0.6 ± 0.0^{b}	0.0426
	length (cm)	28.8 ± 1.9^{a}	23.4 ± 0.9^{a}	19.6 ± 0.4^{b}	< 0.0001
AP + R	total biomass (g)	3.9 ± 0.3^{a}	3.4 ± 0.6^{a}	2.0 ± 0.1^{b}	0.0019
	shoot/root length	0.14 ± 0.01	0.13 ± 0.01	0.13 ± 0.01	0.9819

Data represent the mean of 10 replicates ± SE (standard error)

^{a,b}different letters correspond to significantly different values according to one-way ANOVA ($P < 0.05$), followed by post-hoc Tukey-Kramer test for each treatment

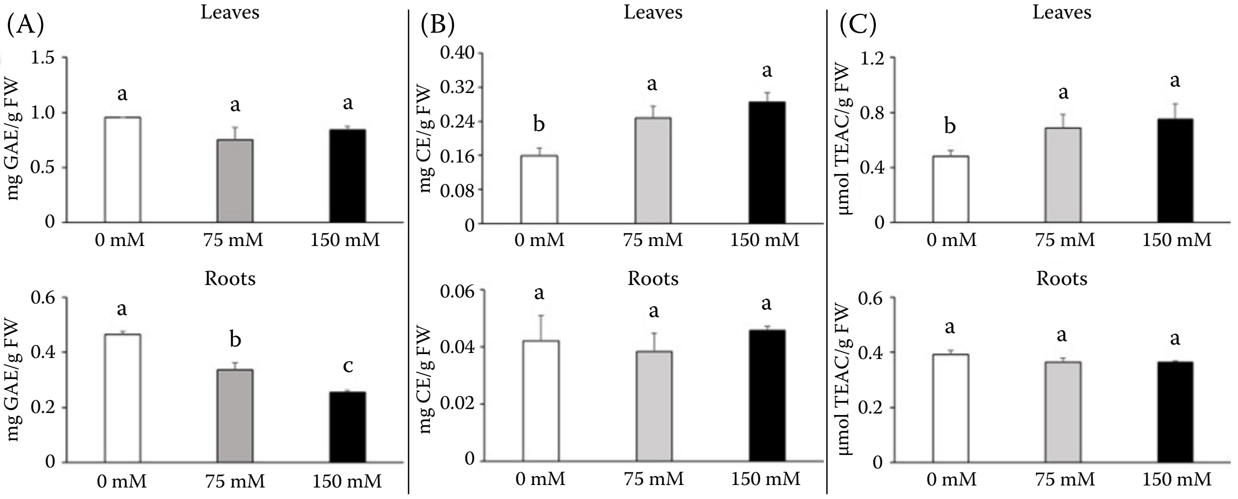

Figure 2. Leaf and root (A) phenols, (B) flavonoids and (C) antioxidant activity of untreated (0 mM) and NaCl-treated (75 mM and 150 mM) tomato plants for 14 days

Data represent the mean of 3 replicates ± SE (standard error)

GAE – gallic acid equivalents; CE – catechin equivalents; TEAC – Trolox equivalent antioxidant capacity; FW – fresh weight

[a,b,c]different letters correspond to significantly different values according to one-way ANOVA (*P* < 0.05), followed by post-hoc Tukey-Kramer test for each treatment

duction compared to the 6 h UV-B-treated plants. Leaf area, leaf FW, and stem length did not show any statistically significant difference between the UV-B-treated and control groups.

At the root level, only FW was affected by 8 h UV-B treatment, which determined a reduction with respect to control and 3 h UV-B-treated plants (–50%). UV-B irradiation did not influence total biomass nor the shoot/root length ratio.

At the leaf level, 8 h UV-B treatment increased the concentration of both phenolic compounds and flavonoids with respect to all treatments, specifically leading to +37% phenols (Figure 3A) and +109% flavonoids (Figure 3B) concentration than in control plants. Consequently, the 8 h UV-B exposure boosted the antioxidant activity (Figure 3C) by 76%, 80%, 94%, and 68% compared to the control. Interestingly, the root phenolics and flavonoid contents were also modulated by UV-B radiation. Indeed, all UV-B treatments caused a significant (ranging from +120% to +160%) increase in total phenols (Figure 3A) if compared to control roots. On the

Table 2. Biometric parameters in tomato plants treated with different UV-B daily doses for 7 days

		UV-B daily doses					
		0 h	1 h	3 h	6 h	8 h	*P*
Aerial part (AP)	leaf area (cm^2)	15.2 ± 1.6	18.8 ± 4.5	17.1 ± 0.8	19.5 ± 2.7	15.5 ± 1.7	0.6504
	leaves (number)	3.2 ± 0.1^a	3.1 ± 0.3^a	3.3 ± 0.2^a	3.3 ± 0.2^a	2.2 ± 0.1^b	**0.0004**
	leaf fresh weight (g)	3.1 ± 0.2	3.2 ± 0.4	3.3 ± 0.3	3.0 ± 0.3	2.5 ± 0.3	0.5327
	stem length (cm)	3.9 ± 0.2	3.3 ± 0.2	3.9 ± 0.2	3.4 ± 0.1	3.8 ± 0.2	0.0546
Roots (R)	fresh weight (g)	1.6 ± 0.2^a	1.5 ± 0.2^{ab}	1.6 ± 0.2^a	1.4 ± 0.2^{ab}	0.8 ± 0.1^b	**0.0223**
	length (cm)	27.0 ± 1.0	25.8 ±1.1	23.8 ± 1.2	24.8 ± 1.5	23.0 ± 1.0	0.1341
AP + R	total biomass (g)	4.6 ± 0.4	4.7 ± 0.3	4.8 ± 0.5	4.4 ± 0.5	3.5 ± 0.4	0.1457
	shoot/root length	0.14 ± 0.01	0.13 ± 0.01	0.17 ± 0.01	0.14 ± 0.02	0.17 ± 0.01	0.0749

Data represent the mean of 10 replicates ± SE (standard error)

[a,b]different letters correspond to significantly different values according to one-way ANOVA (*P* < 0.05), followed by Tukey-Kramer test for each treatment

https://doi.org/10.17221/109/2023-HORTSCI

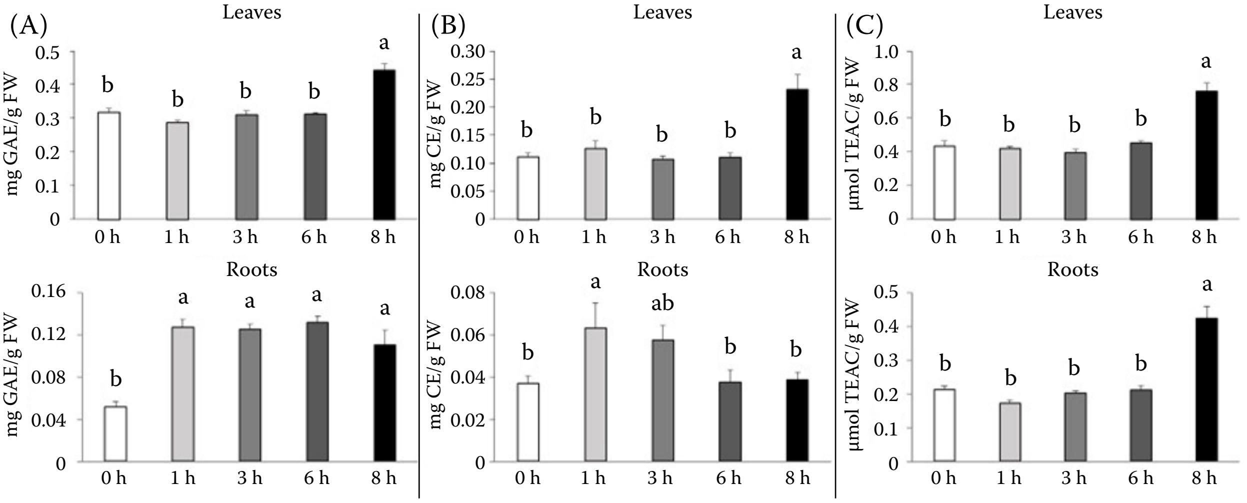

Figure 3. Leaf and root (A) phenols, (B) flavonoids and (C) antioxidant activity of tomato plants treated with different UV-B daily doses

Data represent the mean of 3 replicates ± SE (standard error)

GAE – gallic acid equivalents; CE – catechin equivalents; TEAC – Trolox equivalent antioxidant capacity; FW – fresh weight

^{a,b}different letters correspond to significantly different values following one-way ANOVA ($P < 0.05$), followed by Tukey-Kramer test for each treatment

contrary, flavonoids (Figure 3B) were more concentrated than the control only in the roots of 1 h UV-B-treated plants (+50%). Finally, the antioxidant activity (Figure 3C) was the highest in the roots of 8 h UV-B-treated plants. Particularly, the strongest UV-B exposure determined an increase in root flavonoid concentration by 100, 110, 147% compared to the control and 6 h treatment, 3 h treatment, and 1 h treatment, respectively.

DISCUSSION

Triggering tolerance mechanisms by proper salt treatments

Salinity stress has a negative impact on tomato plant growth, morphology, and physiology (Zhang et al. 2016). In the present study, tomato seedlings were grown in the presence of increasing concentrations of NaCl. Applying 300 mM NaCl, a total inhibition of vegetative growth could be observed (Figure 1), while 150 mM caused a general reduction of the biometric parameters (leaf area and number, stem and root weight, as well as leaf and root length), which is a general symptom of salt stress conditions. The reduction in total leaf area, which was also detected at 75 mM, might be considered a mechanism for minimising water loss by transpiration when the stomata are closed (Acosta-Motos et al. 2017). Indeed, among the salt-related effects on plants, exposure to relatively high NaCl concentrations leads to stomata closure, determining, in turn, a decrease in the photosynthetic rate and the onset of photoinhibition and oxidative stress processes (Loudari et al. 2020). Albacete et al. (2008) described a reduction in leaf area, leaf FW, and root FW in the tomato 'Moneymaker' cultivar grown at 100 mM NaCl after 21 days compared to 0 mM NaCl. The lowest NaCl treatment (75 mM) resulted only in a reduced leaf area with respect to control plants, but no other modifications were observed in the morphological parameters analysed. Also, Bacha et al. (2017) found a decrease in leaf area of the tomato 'Micro-Tom' cultivar after 14 days of 50 mM and 150 mM NaCl, which was correlated with the onset of the oxidative damage, decreased leaf gas exchange and photosynthesis and massive Na^+ accumulation. A similar behaviour was observed in rosemary plants grown at 150 mM NaCl, which displayed a reduced leaf area index compared to control plants (Hamidi-Moghaddam et al. 2019). However, we observed no modification in the shoot/root length ratio at both 75 mM and 150 mM NaCl, while these authors found a lower ratio with respect to 0 mM NaCl rosemary plants, meaning that, in our experiment, there was no reallocation of resources to the root system.

In this study, biochemical analyses were performed in the upper- and below-ground organs, and revealed

https://doi.org/10.17221/109/2023-HORTSCI

the modification of the phenolic metabolism in response to salt stress, at both levels. Contrary to our findings, some studies (Al Hassan et al. 2015; Bacha et al. 2017) reported an increase in the leaf phenolic content in plants subjected to salinity stress, but they did not investigate the root part. In our experiment, the reduction of total phenols in roots, which decreases progressively according to different NaCl concentrations, could be ascribed to the consumption of these metabolites in order to counteract the oxidative stress induced by salinity. Phenolic compounds play a variety of roles in plants, ranging from constituents (lignin) to development and growth modulators. The flavonoid subgroup is the largest and most complex subgroup of phenolic compounds, and it plays an important role in biotic and abiotic stress defence. In leaves, flavonoid concentrations increased with 75 mM and 150 mM NaCl, which is in accordance with Al Hassan et al. (2015). Also, the antioxidant activity followed the trend of foliar flavonoids. Based on our results, 75 mM NaCl applied for 14 days could be a proper dose to boost the non-enzymatic antioxidant system of tomato plants without heavily altering the plant growth and development. Thus, the application of mild salt treatments could be a feasible technique in the optics of increasing the tolerance of plants to salinity conditions before being transplanted in salt-affected soils. Moreover, one of the great problems affecting farmers worldwide is the salinisation of water resources (Colombani 2022). Our results showed the possibility of watering 'Moneymaker' tomato seedlings with slightly saline water.

UV-B treatments as a booster of the plant non-enzymatic antioxidant defences

UV-B treatment only affected the number of leaves and root weight when seedlings were exposed to the highest dose (8 h per day). In line with our results about the decrease of root biomass by the 8 h UV-B treatment, Lee et al. (2021) described a reduction in the root FW of 'New Red Fire' lettuce treated with UV-B radiation (1.97 W/m^2) for 5 days. These results confirm the ability of UV-B to impact the growth and architecture of the root apparatus, although not directly exposed to the UV-B radiation. We detected only another negative effect of the 8 h UV-B treatment on the growth and morphology of tomato plants, consisting of the decreased number of leaves. However, the UV-B-induced morphological changes are often contradictory, as reported in other studies (Caldwell et al. 2007; Hamidi-Moghaddam et al. 2019), and are strictly related to both the plant species and cultivar analysed, as well as the light regimen (intensity and spectral composition) and the UV-B experimental conditions adopted. Indeed, when UV-B radiation is applied at high doses, it might negatively affect plant growth and biomass production due to the UV-B-induced damage in the photosynthetic machinery and, generally, in many cell cycle processes, e.g. DNA replication and repair mechanisms (Biever et al. 2014; Cuzzuol et al. 2020; Kosobryukhov et al. 2020; Yadav et al. 2020). A reduction in plant growth was in fact observed in many plant species, e.g. basil, potato, and flaxseed (Dou et al. 2019; Chen et al. 2020; Santin et al. 2022). However, some other works have found an increase in some biometric indices after the UV-B exposure, e.g. in lettuce plants (Santin et al. 2023), likely due to the low and ecologically relevant UV-B doses applied in comparison with what is reported in the other studies. The UV-B treatment did not induce any changes in leaf area, in agreement with the observations of Alexieva et al. (2001) on pea (*Pisum sativum* L., 'Citrina' cultivar) and wheat seedlings (*Triticum aestivum* L., 'Centauro' cultivar) treated with UV-B for 2 h for 7 days (corresponding to 49 kJ/m^2/day). Therefore, the absence of UV-B-induced significant results in terms of leaf area, leaf FW, and stem length indicated that the UV-B doses applied to tomato plants did not induce heavy impairments in the plant development.

Considering the plant's non-enzymatic antioxidant system, a daily UV-B exposure of 8 h for 7 days led to an increase in total phenolics and flavonoids in the leaf and, therefore, a boost in the leaf antioxidant capacity. The same trend was also evident in roots, except for the flavonoids response. In line with our results, Mannucci et al. (2020) irradiated the tomato 'Micro-Tom' cultivar with 15 min UV-B/day (corresponding to 1.19 kJ/m^2) for 8 days, recorded a similar accumulation of phenols and flavonoids concentration in leaves, but not in roots. These results suggested that exposing tomato plantlets to UV-B radiation for 8 h/day in controlled conditions might improve the non-enzymatic antioxidant defences, helping them to promptly face and counteract possible other environmental stress once transplanted in the field, both abiotic (e.g. drought, salt, heat, heavy metals) and biotic (e.g. bacteria, viruses, insects, pests) ones (Tak, Kumar 2020). Also, Alexieva et al. (2001) observed an increase in total phenols after UV-B irradiation for 2 h for 7 days in wheat and pea leaves. Indeed, phenolics and flavonoids are well-known phytochemicals that are able to prevent oxidative damage due to ROS that might be overproduced as a consequence of biotic and abiotic factors. Additionally, these compounds act as UV-B-absorbing substances in the epidermal cell layers, reducing the transmission of this wavelength to the mesophyll and thereby defending the photosystems (Burchard et al. 2000; Mannucci et al. 2022).

CONCLUSION

The results of this study suggest that the application of mild abiotic treatments, namely a salt treatment (75 mM, 14 days) or a UV-B exposure (8 h/day corresponding to 18.43 kJ/m^2, 7 days) to hydroponically grown tomato seedlings can increase the content of foliar total phenolics and flavonoids without inducing strong impairments in the plant growth and development. Interestingly, this work provides evidence that the UV-B radiation, although perceived only by the above-ground organs of the plants, also induces some morphological and biochemical changes in the root system. In conclusion, these findings might pave the way for applying mild salt and UV-B treatments on early-stage tomato plants in controlled conditions to increase their biochemical defences and therefore their resistance towards the environmental conditions and possible stresses they might have to face once transferred to the open field.

REFERENCES

Acosta-Motos J.R., Ortuño M.F., Bernal-Vicente A., Diaz-Vivancos P., Sanchez-Blanco M.J., Hernandez J.A. (2017): Plant responses to salt stress: Adaptive mechanisms. Agronomy, 7: 18.

Alexieva V., Sergiev I., Mapelli S., Karavov E. (2001): The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant Cell and Environment, 24: 1337–1344.

Albacete A., Ghanem M.E., Martínez-Andújar C., Acosta M., Sánchez-Bravo J., Martínez V., Lutts S., Dodd I.C., Pérez-Alfocea F. (2008): Hormonal changes in relation to biomass partitioning and shoot growth impairment in salinized tomato (*Solanum lycopersicum* L.) plants. Journal of Experimental Botany, 59: 4119–4131.

Al Hassan M., Fuertes M.M., Sánchez F.J.R., Vicente O., Boscaiu M. (2015): Effects of salt and water stress on plant growth and on accumulation of osmolytes and antioxidant compounds in cherry tomato. Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 43: 1–11.

Bacha H., Tekaya M., Drine S., Guasmi F., Touil L., Enneb H., Triki T., Cheour F., Ferchichi A. (2017): Impact of salt stress on morpho-physiological and biochemical parameters of *Solanum lycopersicum* cv. Microtom leaves. South African Journal of Botany, 108: 364–369.

Biever J.J., Brinkman D., Gardner G. (2014): UV-B inhibition of hypocotyl growth in etiolated *Arabidopsis thaliana* seedlings is a consequence of cell cycle arrest initiated by photodimer accumulation. Journal of Experimental Botany, 65: 2949–2961.

Borbalàn A.M.A., Zorro L., Guillen D.A., Barroso C.G. (2003): Study of the polyphenol content of red and white grape varieties by liquid chromatography-mass spectrometry and its relationship to antioxidant power. Journal of Chromatography A, 1012: 31–38.

Burchard P., Bilger W., Weissenböck G. (2000): Contribution of hydroxycinnamates and flavonoids to epidermal shielding of UV-A and UV-B radiation in developing rye primary leaves as assessed by ultraviolet-induced chlorophyll fluorescence measurements. Plant Cell and Environment, 23: 1373–1380.

Brown B.A., Cloix C., Jiang G., Kaiserli E., Herzyk P., Kliebenstein D.J., Jenkins G.I. (2005): A UV-B-specific signaling component orchestrates plant UV protection. Proceedings of the National Academy of Sciences (PNAS), 102: 18225–18230.

Caldwell M.M., Bornman J.F., Ballaré C.L., Flint S.D., Kulandaivelu G. (2007): Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. Photochemical and Photobiological Sciences, 6: 252–266.

Chen Z., Gao W., Reddy K.R., Chen M., Taduri S., Meyers S.L., Shankle M.W. (2020): Ultraviolet (UV) B effects on growth and yield of three contrasting sweet potato cultivars. Photosynthetica, 5: 37–44.

Clayton W.A., Albert N.W., Thrimawithana A.H., McGhie T.K., Deroles S.C., Schwinn K.E., Warren B.A., McLachlan A.R.G., Bowman J.L., Jordan B.R., Davies K.M. (2018): UVR8-mediated induction of flavonoid biosynthesis for UVB tolerance is conserved between the liverwort *Marchantia polymorpha* and flowering plants. Plant Journal, 96: 503–517.

Colombani N. (2022): Special issue "Salinization of water resources: Ongoing and future trends". Water, 14: 1806.

Crestani G., Cunningham N., Csepregi K., Uthman O.B., Marcel A.K. (2023): From stressor to protector, UV-induced abiotic stress resistance. Photochemical & Photobiological Sciences, 22: 2189–2204.

Cuzzuol G.R.F., Gama V.N., Zanetti L.V., Werner E.T., Pezzopane J.E.M. (2020): UV-B effects on growth, photosynthesis, total antioxidant potential and cell wall components of shade-tolerant and sun-tolerant ecotypes of *Paubrasilia echinata*. Flora, 271: 151679.

Daryanavard H., Postiglione A.E., Mühlemann J.K., Muday G.K. (2023): Flavonols modulate plant development, signaling, and stress responses. Current Opinion in Plant Biology, 72: 102350.

Demkura P.V., Ballare C.L. (2012): UVR8 mediates UV-B-induced *Arabidopsis* defense responses against *Botrytis cinerea* by controlling sinapate accumulation. Molecular Plant, 5: 642–652.

Dhanya Thomas T.T., Puthur J.T. (2017): UV radiation priming: a means of amplifying the inherent potential for abiotic stress tolerance in crop plants. Environmental and Experimental Botany, 138: 57–66.

Dhanya Thomas T.T., Dinakar C., Puthur J.T. (2020): Effect of UV-B priming on the abiotic stress tolerance of stress-sensitive rice seedlings: Priming imprints and cross-tolerance. Plant Physiology and Biochemistry, 147: 21–30.

Dou H., Niu G., Gu M. (2019): Pre-harvest UV-B radiation and photosynthetic photon flux density interactively affect plant photosynthesis, growth, and secondary metabolites accumulation in basil (*Ocimum basilicum*) plants. Agronomy, 9: 434.

Easlon H.M., Bloom A.J. (2014): Easy Leaf Area: Automated digital image analysis for rapid and accurate measurement of leaf area. Applications in Plant Sciences, 2: 1400033.

Fedoroff N.V., Battisti D.S., Beachy R.N., Cooper P.J., Fischhoff D.A., Hodges C.N., Knauf V.C., Lobell D., Mazur B.J., Molden D., Reynolds M.P., Ronald P.C., Rosegrant M.W., Sanchez P.A., Vonshak A., Zhu J.K. (2010): Radically rethinking agriculture for the 21st century. Science, 327: 833–834.

Ferreira-Silva S.L., Voigt E.L., Silva E.N., Maia J.M., Aragão T.C.R., Silveira J.A.G. (2012): Partial oxidative protection by enzymatic and non-enzymatic components in cashew leaves under high salinity. Biologia Plantarum, 56: 172–176.

Hamidi-Moghaddam A., Arouiee H., Moshtaghi N., Azizi M., Shoor M., Sefidkon F. (2019): Visual quality and morphological responses of rosemary plants to UV-B radiation and salinity stress. Journal of Ecological Engineering, 20: 34–43.

Hassani A., Azapagic A., Shokri N. (2020): Predicting long-term dynamics of soil salinity and sodicity on a global scale. Proceedings of the National Academy of Sciences (PNAS). 117: 33017–33027.

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. Journal of Agricultural and Food Chemistry, 51: 6509–6515.

Kosobryukhov A., Khudyakova A., Kreslavski V. (2020): Impact of UV radiation on photosynthetic apparatus: Adaptive and damaging mechanisms. In: Hasanuzzaman M. (ed.): Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives I. Singapore, Springer: 555–576.

Lee M., Rivard C., Pliakoni E., Wang W., Rajashekar C.B. (2021): Supplemental UV-A and UV-B affect the nutritional quality of lettuce and tomato: Health-promoting phytochemicals and essential nutrients. American Journal of Plant Sciences, 12: 104–126.

Loudari A., Benadis C., Naciri R., Soulaimani A., Zeroual Y., Gharous M.E., Kalaji H.M., Oukarroum A. (2020): Salt stress affects mineral nutrition in shoots and roots and chlorophyll a fluorescence of tomato plants grown in hydroponic culture. Journal of Plant Interactions, 15: 398–405.

Mannucci A., Mariotti L., Castagna A., Santin M., Trivellini A., Reyes T.H., Mensuali-Sodi A., Ranieri A., Quartacci M.F. (2020): Hormone profile changes occur in roots and leaves of Micro-Tom tomato plants when exposing the aerial part to low doses of UV-B radiation. Plant Physiology and Biochemistry, 148: 291–301.

Mannucci A., Santin M., Vanhaelewyn L., Sciampagna M.C., Miras-Moreno M.B., Zhang L., Lucini L., Quartacci M.F., Van Der Straeten D., Castagna A., Ranieri A. (2022): Foliar and root comparative metabolomics and phenolic profiling of Micro-Tom tomato (*Solanum lycopersicum* L.) plants associated with a gene expression analysis in response to short daily UV treatments. Plants, 11: 1829.

McLay E.R., Pontaroli A.C., Wargent J.J. (2020): UV-B induced flavonoids contribute to reduced biotrophic disease susceptibility in lettuce seedlings. Frontiers in Plant Science, 11: 594681.

Meyer P., Van de Poel B., De Coninck B. (2021): UV-B light and its application potential to reduce disease and pest incidence in crops. Horticulture Research 8: 194.

Nadeem M., Anwar-ul-Haq M., Saqib M., Maqsood M., He Z. (2022): Ameliorative effect of silicic acid and silicates on oxidative, osmotic stress, and specific ion toxicity in spring wheat (*Triticum aestivum* L.) genotypes. Journal of Soil Science and Plant Nutrition, 22: 2334–2345.

Naveed M., Sajid H., Mustafa A., Niamat B., Ahmad Z., Yaseen M., Kamran M., Rafique M., Ahmar S., Chen J.T. (2020): Alleviation of salinity-induced oxidative stress, improvement in growth, physiology and mineral nutrition of canola (*Brassica napus* L.) through calcium-fortified composted animal manure. Sustainability, 12: 846.

Negrão S., Schmöckel S.M., Tester M. (2017): Evaluating physiological responses of plants to salinity stress. Annals of Botany, 119: 1–11.

Raza A., Razzaq A., Mehmood S.S., Zou X., Zhang X., Lv Y., Xu J. (2019): Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. Plants, 8: 34.

Re R., Pellegrini N., Proteggente A., Pannala A., Yang M., Rice-Evans C. (1999): Antioxidant activity applying an improved ABTS radical cation decolorization assay. Free Radical Biology and Medicine, 26: 1231–1237.

Robson T.M., Klem K., Urban O., Jansen M.A. (2015): Re-interpreting plant morphological responses to UV-B radiation. Plant, Cell and Environment, 38: 856–866.

Roșca M., Mihalache G., Stoleru V. (2023): Tomato responses to salinity stress: From morphological traits to genetic changes. Frontiers in Plant Science, 14: 1118383.

Santin M., Ranieri A., Castagna A. (2021): Anything new under the sun? An update on modulation of bioactive compounds by different wavelengths in agricultural plants. Plants, 10: 1485.

Santin M., Sciampagna M.C., Mannucci A., Puccinelli M., Angelini L.G., Tavarini S., Accorsi M., Incrocci L., Ranieri A., Castagna A. (2022): Supplemental UV-B exposure influences the biomass and the content of bioactive compounds in *Linum usitatissimum* L. sprouts and microgreens. Horticulturae, 8: 213.

Santin M., Zeni V., Grassi A., Ricciardi R., Pieracci Y., Di Giovanni F., Panzani S., Frasconi C., Agnolucci M., Avio L., Turrini A., Giovannetti M., Ruffini Castiglione M., Ranieri A., Canale A., Lucchi A., Agathokleous E., Benelli G. (2023): Do changes in *Lactuca sativa* metabolic performance, induced by mycorrhizal symbionts and leaf UV-B irradiation, play a role towards tolerance to a polyphagous insect pest? Environmental Science and Pollution Research, 30: 56207–56223.

Tak Y., Kumar M. (2020): Phenolics: A key defence secondary metabolite to counter biotic stress. Plant Phenolics in Sustainable Agriculture, 1: 309–329.

Tavarini S., Castagna A., Conte G., Foschi L., Sanmartin C., Incrocci L., Ranieri A., Serra A., Angelini L.G. (2019): Evaluation of chemical composition of two linseed varieties as sources of health-beneficial substances. Molecules, 24: 3729.

Yadav A., Singh D., Lingwan M., Yadukrishnan P., Masakapalli S.K., Datta S. (2020): Light signaling and UV-B-mediated plant growth regulation. Journal of Integrative Plant Biology, 62: 1270–1292.

Zhang P., Senge M., Dai Y. (2016): Effects of salinity stress on growth, yield, fruit quality and water use efficiency of tomato under hydroponics system. Reviews in Agricultural Science, 4: 46–55.

Zhu J.K. (2016): Abiotic stress signaling and responses in plants. Cell, 167: 313–324.

Received: September 27, 2023
Accepted: April 23, 2025