Impact of Short-Term Waterlogging Stress on Plant Morphology, Chlorophyll and Carotenoid Contents of Summer Tomato

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Abstract: Waterlogging is an increasingly important constraint to tomato (*Solanum lycopersicum* L.) production, particularly during the summer season in Bangladesh, where intense rainfall and transient flooding frequently coincide with crop growth. This study evaluated the morphological, physiological and fruit-quality responses of three BARI-developed summer tomato hybrids exposed to short-term waterlogging (water maintained 15 cm above the soil surface for three consecutive days at 45 days after transplanting). Across nine measured traits, waterlogging significantly reduced most growth, water-status and yield-related parameters, while proline increased markedly as a generalized stress response. Significant genotype × treatment interactions were detected for shoot length, root length and fruit yield, indicating genotype-specific responses for these traits. BARI Hybrid Tomato-10 was consistently the most sensitive genotype, whereas BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 maintained comparatively better growth and yield under waterlogging. BARI Hybrid Tomato-08 showed the smallest proportional yield reduction (1.31 to 1.29 kg plant^{-1}), while BARI Hybrid Tomato-11 showed the most stable fruit lycopene content. Because the experiment included only three genotypes and one short-duration stress episode, these results should be interpreted as a preliminary controlled-condition screen. BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 are recommended for further multi-season and field-based validation under transient waterlogging conditions.
Keywords: *Solanum lycopersicum*, waterlogging stress, chlorophyll, proline, carotenoids, tomato yield, abiotic stress tolerance

Introduction

Waterlogging due to excessive and unregulated heavy rainfall events has found its place as one of the most common and destructive natural disasters. It negatively affect agricultural production worldwide, mainly due to climate change and extreme weather conditions (Voesenek et al., 2015). Approximately 16% of arable land worldwide and more than 21% of arable land in Bangladesh are affected by waterlogging conditions (Hagage et al., 2024; Khan & Shoumik, 2022). The trend is expected to deteriorate due to extreme weather conditions caused by climate change and extreme heavy rainfall events. Tomato is one of the major vegetable crops that grow widely around the globe. Asia, America, Europe, and Africa contributed approximately 54.9%, 17.3%, 15.5%, and 11.9%, of tomato production worldwide respectively, on average from 1994 to 2021 (FAO, 2022). It is one of the largest and popular vegetable crops in Bangladesh. It ranks fourth in terms of production and third in terms of area of production in Bangladesh (Ferdous et al., 2017). In winter season it grows well due to favorable environmental conditions. However, it possesses an enormous opportunity of growing in summer too.
Due to its diversified uses, taste, colour, and high nutritive values, the demand is growing day-by-day. However, the production is quite short especially during the summer season. (Mondal et al., 2011; Rathore et al., 2021). With the growing demand and importance of tomatoes, the Bangladesh Agricultural Research Institute (BARI) has developed only a few varieties of tomatoes during the off-

season and summer. Summer tomato production in Bangladesh has the possibility of being a vital enterprise as the production of the summer tomato is highly profitable and demanded (Zaman et al., 2006). However, the production of the summer tomato is affected by the heavy rainfall, floods, wind storms, and other conditions during the monsoon periods. Tomatoes are highly susceptible to waterlogging stress especially because the vegetative and generative parts of tomatoes are adversely affected by the stress (Mohanty et al., 2020). The short-term waterlogging stress (up to three days) has a great impact on the flowering and fruit maturation of the tomato plants, which finally led to the significantly reduced tomato production (Yin et al., 2023). With the growing importance and demand of the summer tomatoes, there is a need for further work in understanding the physiological and biochemical responses of the tomato plants during the waterlogging stress. Thus, the study is assigned to explore the effects of short-term waterlogging stress on the plant morphology, chlorophyll, and carotenoid content of the summer tomatoes and to identify the best variety suitable for the growing in summer.

Materials and Methods

Plant Materials and Growth Conditions

The seeds of three hybrids of tomato plants (*Solanum lycopersicum* L.) namely BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11 were collected from the Bangladesh Agricultural Research Institute (BARI). The seeds were germinated in pots with a universal soil mix and kept under natural conditions in the Biotechnology Laboratory, Faculty of Agriculture, Patuakhali Science and Technology University, Bangladesh. The experimental design was a factorial completely randomized design with three replications. When the plants were 45 days old, waterlogging stress for a short term was applied by keeping the water level of 15 cm above the soil surface for 3 consecutive days. Watering stopped, and the plants were allowed to recover under natural conditions until the plants attained reproductive maturity.

The following important parameters were assessed to examine the physiological and biochemical responses of the tomato plants under short-term waterlogging stress.

Table 1. Parameters measured to assess plant growth performance under short-term waterlogging stress

Parameter	Description	Measurement
Shoot length	Length of the above-ground stem from the base to the apical meristem, expressed in cm	Measured with a ruler from the soil surface to the shoot apex at the end of the treatment period
Root length	Length of the primary root from the root–shoot junction to the root tip, expressed in cm	Measured with a ruler after careful removal of roots from the growth medium and gentle rinsing
Number of leaves	Total count of fully expanded leaves per plant at the time of harvest	Manual count of all expanded leaves per individual plant
Relative water content (RWC)	The ratio of actual water content to the water content at full turgidity, expressed as a percentage. Calculated as: RWC (%) = [(FW − DW) / (TW − DW)] × 100, where FW = fresh weight, TW = turgid weight after floating on distilled water for 24 h at 4 °C in the dark, and DW = dry weight after oven-drying at 80 °C for 48 h. The procedure was repeated thrice for each replicate.	RWC was estimated following the procedure of Barrs & Weatherley (1962).

Chlorophyll content (SPAD value)	Relative index of leaf chlorophyll concentration based on light transmittance at 650 nm and 940 nm. It is expressed as SPAD value. Higher values indicate greater chlorophyll content and photosynthetic potential	Non-destructive readings with a SPAD-502 Plus Chlorophyll Meter (Konica Minolta, Japan).Three readings per plant taken on the adaxial surface of fully expanded leaves; values were then averaged to get one SPAD value per plant

Biochemical Analyses

Proline analysis: Proline content was determined by the ninhydrin-colorimetric assay described by Ábrahám et al. (2010). Leaf material was homogenized in 2 mL of 3% sulfosalicylic acid, boiled in water for 10 min and centrifuged; the supernatant was treated with glacial acetic acid and acidic ninhydrin reagent and boiled again for 30 min. Toluene was then added, and the toluene phase was separated and measured for absorbance at 520 nm with a UV-Vis spectrophotometer. Proline concentration was estimated from a standard curve of known L-proline concentrations and expressed as $\mu mol\ g^{-1}$ fresh weight (FW).

Lycopene and β-carotene Estimation

Quantification of lycopene and β-carotene used a modified spectrophotometric method based on Fraser et al. (2000) and Lichtenthaler (1987). Fresh tomato fruit tissue (0.5 g) was extracted in hexane:acetone:ethanol (2:1:1, v/v/v) containing 0.05% butylated hydroxytoluene to inhibit oxidative breakdown. The extract was vortexed for 1 min, kept in the dark at room temperature for 15 min, then centrifuged at 5,000 rpm for 10 min; the upper organic phase was collected. Absorbance was recorded at 503 nm for lycopene and 472 nm for β-carotene using a Genesys 10S UV-Vis spectrophotometer (Thermo Fisher Scientific, USA). Pigment contents were calculated using the extinction coefficients lycopene $\varepsilon = 17.2 \times 10^4\ M^{-1}\ cm^{-1}$ at 503 nm and β-carotene $\varepsilon = 13.9 \times 10^4\ M^{-1}\ cm^{-1}$ at 472 nm (Zechmeister et al., 1941; Fish et al., 2002) and expressed as $mg\ g^{-1}$ FW. Each sample was measured in triplicate, with solvent blanks for calibration.

Waterlogging Tolerance Index (WTI) Estimation

For each trait, WTI was computed as (waterlogged mean / control mean) × 100. Genotypes with WTI ≥ 90% were classified as tolerant for that trait, 80–89% as moderately tolerant, and < 80% as sensitive. For growth, water-status, pigment and yield traits, higher WTI values indicate stronger trait retention under waterlogging. Proline was interpreted separately because it increased under stress; its WTI therefore reflects stress-response magnitude rather than tolerance.

Statistical analysis

Data were analysed using two-way factorial ANOVA with genotype (G), treatment (T) and the G × T interaction as fixed effects, testing: (i) the overall effect of waterlogging, (ii) differences among genotypes and (iii) whether genotypes differed in their response to waterlogging. Tukey's HSD test ($p \leq 0.05$) was used for post-hoc mean separation among genotypes within each treatment. To directly compare control and waterlogged plants within each genotype, Welch's two-sample t-test was performed for each trait × genotype combination. Pearson correlation coefficients were calculated among traits under the waterlogged condition. Because the correlation analysis was based on nine genotype-treatment replicate observations, correlations were interpreted cautiously and both unadjusted and Bonferroni-adjusted significance were considered. All analyses were performed in R (version 4.6.0). Graphical visualizations were done using appropriate R packages.

Results

Two-way factorial ANOVA for the nine measured traits is presented in Table 2. Treatment had a significant main effect on all traits except β-carotene, whereas genotype had a significant main effect on seven of the nine traits. Significant genotype × treatment interactions were detected for shoot length, root length, and fruit yield, indicating that these traits differed in their response to waterlogging among genotypes. The remaining traits showed non-significant genotype × treatment interactions. Within-genotype CK vs WL comparisons (Welch's two-sample t-test) for each of the nine traits are reported in Table 3.

Table 2. Two-way factorial analysis of variance (ANOVA) for nine traits under control and short-term waterlogging conditions

Trait	**Source of variation**	**df**	**F value**	***p value***	**Significance**
Chlorophyll content (SPAD value)	Genotype (G)	2	0.44	0.655	ns
	Treatment (T)	1	66.55	< 0.001	***
	G × T	2	0.78	0.480	ns
Shoot length (cm)	Genotype (G)	2	45.92	< 0.001	***
	Treatment (T)	1	107.06	< 0.001	***
	G × T	2	23.98	< 0.001	***
Root length (cm)	Genotype (G)	2	10.32	0.003	**
	Treatment (T)	1	32.77	< 0.001	***
	G × T	2	3.98	0.047	*
Number of leaves	Genotype (G)	2	8.04	0.006	**
	Treatment (T)	1	32.14	< 0.001	***
	G × T	2	2.68	0.109	ns
Leaf RWC (%)	Genotype (G)	2	10.04	0.003	**
	Treatment (T)	1	36.82	< 0.001	***
	G × T	2	3.07	0.084	ns
Proline (μmol g^{-1} FW)	Genotype (G)	2	0.65	0.540	ns
	Treatment (T)	1	787.06	< 0.001	***
	G × T	2	0.20	0.820	ns
Lycopene (mg/g FW)	Genotype (G)	2	5.54	0.020	*
	Treatment (T)	1	9.91	0.008	**
	G × T	2	1.93	0.188	ns
β-carotene (mg/g FW)	Genotype (G)	2	8.87	0.004	**

Trait	Source of variation	df	F value	*p value*	Significance
	Treatment (T)	1	4.36	0.059	ns
	G × T	2	0.07	0.929	ns
Fruit yield (kg plant^{-1})	Genotype (G)	2	32.37	< 0.001	***
	Treatment (T)	1	26.33	< 0.001	***
	G × T	2	5.96	0.016	*

*Significance levels: *** p < 0.001; ** p < 0.01; * p < 0.05; ns = non-significant (p ≥ 0.05).*

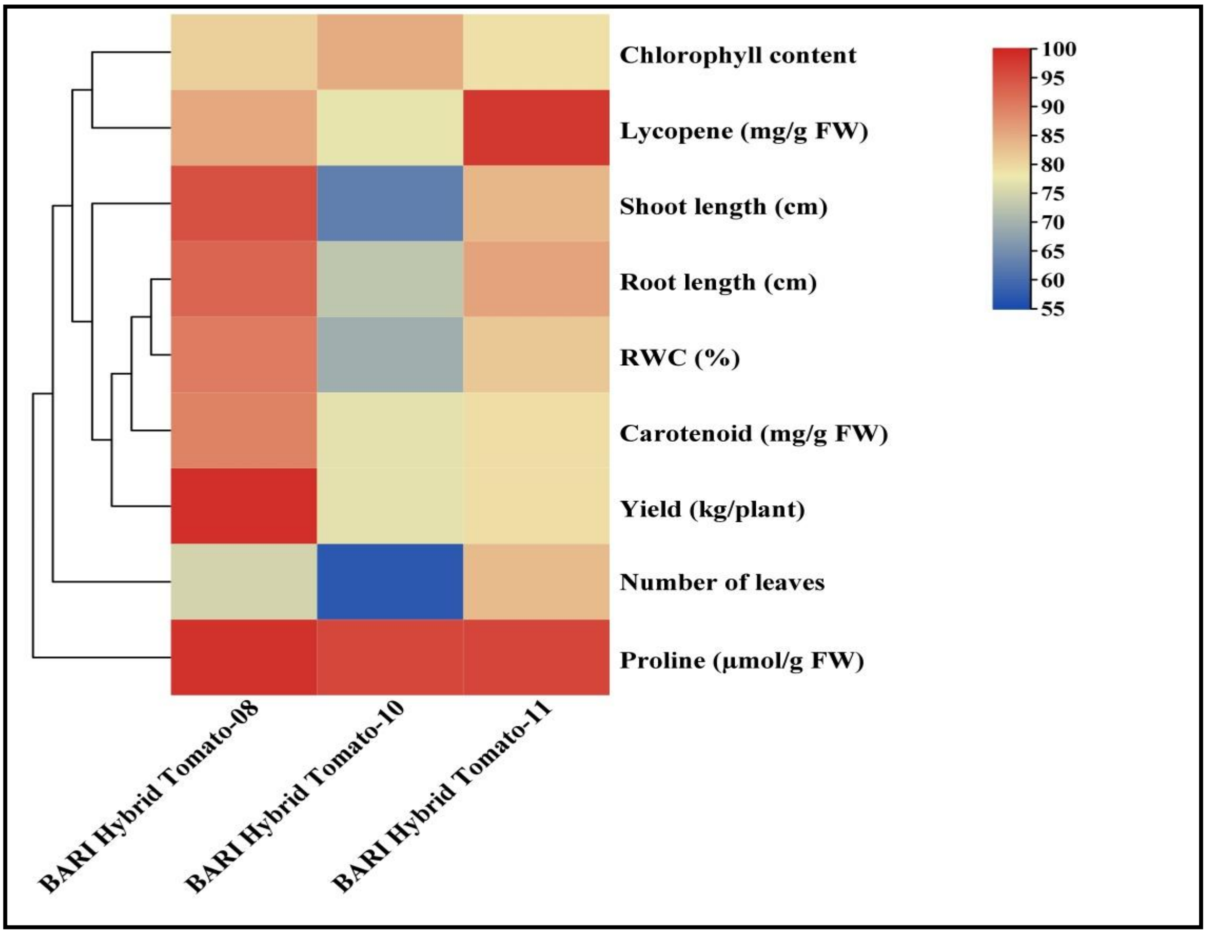

Figure 1. Heatmap of the Waterlogging Tolerance Index (WTI) in three BARI Hybrid Tomato genotypes. *Note*: Proline accumulates in response to stress rather than declining, so here its WTI is interpreted as a stress-marker rather than a tolerance score.

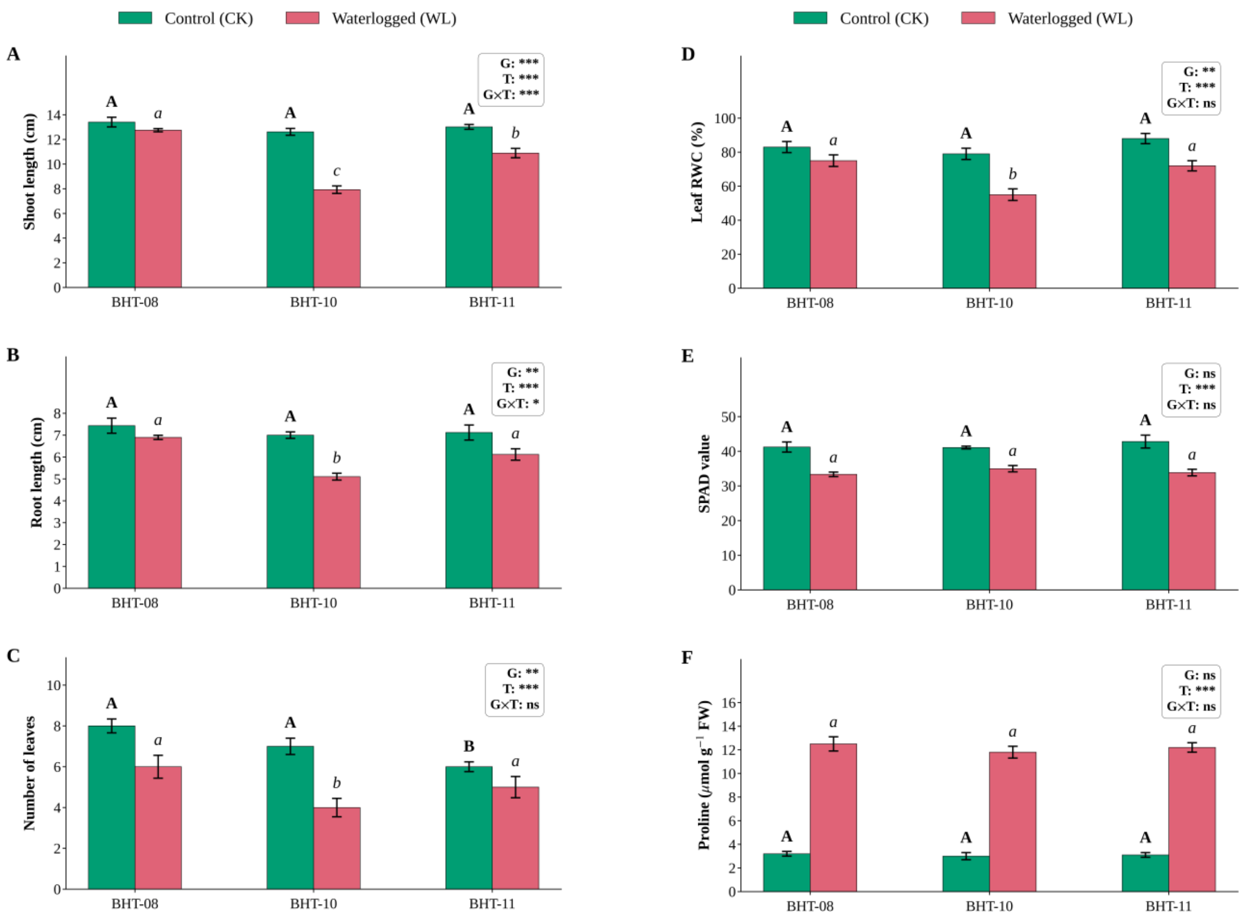

Figure 2. Effects of genotype (G), waterlogging treatment (T), and their interaction (G × T) on growth and physiological traits of three Tomato genotypes under control (CK) and waterlogged (WL) conditions. Bars represent mean ± standard error of three biological replicates. *, **, and *** indicate significance at $p < 0.05$, 0.01, and 0.001, respectively; ns = non-significant.

Effect of Waterlogging on Chlorophyll Content (SPAD)

The ANOVA results revealed that short-term waterlogging stress significantly reduced leaf chlorophyll content (Table 2). This reduction was observed across all three genotypes (Treatment effect, $p < 0.001$). However, a non-significant genotype main effect ($p = 0.655$) and the G × T interaction ($p = 0.480$) were observed across genotypes. These results indicate that the chlorophyll content in leaf was reduced to a comparable extent under this stress. Mean SPAD values declined from 41.2 ± 1.5 to 33.4 ± 0.7 in BARI Hybrid Tomato-08 (a 19.1 % reduction), from 41.1 ± 0.4 to 35.0 ± 0.9 in BARI Hybrid Tomato-10 (14.9 %), and from 42.8 ± 1.9 to 33.9 ± 1.0 in BARI Hybrid Tomato-11 (20.9 %) (Figure 2E). Moreover, the corresponding waterlogging tolerance index (WTI = WL/CK × 100) values were 80.9 %, 85.1 %, and 79.1 % for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11, respectively (Figure 1).

Effect of Waterlogging on Leaf Number

A significant variation was found in the number of leaves among all genotypes under short-term waterlogging stress ($p < 0.001$), and a significant Genotype main effect was also observed ($p = 0.006$). However, the interaction was not found significant ($p = 0.109$) among the treatments and genotypes. It is important to distinguish two separate measures: (i) the number of leaves retained under stress (absolute), and (ii) the proportional loss relative to each genotype's own control (WTI). The result was presented in Figure 2C. Under Control conditions, BARI Hybrid Tomato-08 had the most leaves (8.0 ± 0.3), followed by BARI Hybrid Tomato-10 (7.0 ± 0.4) and BARI Hybrid Tomato-11 (6.0 ± 0.2). Under Waterlogging, BARI Hybrid Tomato-08 retained the highest absolute leaf number (6.0 ± 0.6), but its WTI (75.0%) was lower than BARI Hybrid tomato-11's WTI (83.3%), indicating BARI Hybrid Tomato-11 lost a smaller proportion of its leaves relative to its own control. BARI Hybrid Tomato-10 showed the greatest reduction in both absolute terms and proportionally (WTI = 57.1%).

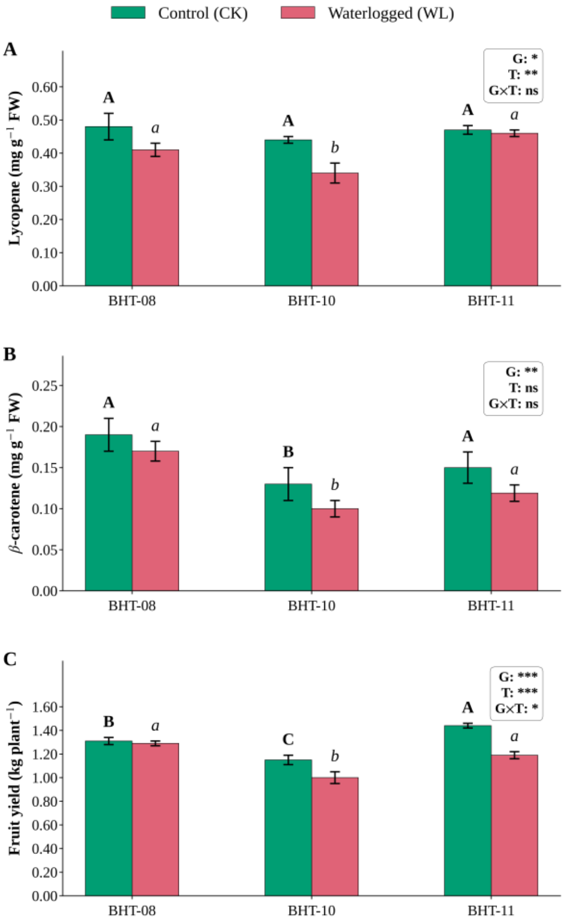

Figure 3. Effects of genotype (G), waterlogging treatment (T), and their interaction (G × T) on fruit quality and yield traits of three BARI Hybrid Tomato genotypes under control (CK) and waterlogged (WL) conditions. (A) lycopene, (B) β-carotene, (C) fruit yield. Bars represent mean ± standard error of three biological replicates. *, **, and *** indicate significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, and ns indicates non-significance.

Table 3. Within-genotype comparison of control (CK) and waterlogged (WL) conditions for the nine traits measured in three BARI Hybrid Tomato genotypes.

Trait	Genotype	CK Mean ± SE	WL Mean ± SE	% Change	p value	Sig.
Chlorophyll content (SPAD Value)	BARI Hybrid Tomato-08	41.23 ± 1.47	33.35 ± 0.66	−19.1	0.020	*
	BARI Hybrid Tomato-10	41.09 ± 0.40	34.98 ± 0.90	−14.9	0.011	*
	BARI Hybrid Tomato-11	42.81 ± 1.86	33.86 ± 0.95	−20.9	0.024	*
Shoot Length (cm)	BARI Hybrid Tomato-08	13.41 ± 0.39	12.75 ± 0.13	−4.9	0.229	ns
	BARI Hybrid Tomato-10	12.62 ± 0.28	7.93 ± 0.30	−37.2	<0.001	***
	BARI Hybrid Tomato-11	13.02 ± 0.20	10.89 ± 0.38	−16.3	0.016	*

Root Length (cm)	BARI Hybrid Tomato-08	7.43 ± 0.35	6.90 ± 0.10	−7.2	0.257	ns
	BARI Hybrid Tomato-10	7.00 ± 0.15	5.10 ± 0.16	−27.1	<0.001	***
	BARI Hybrid Tomato-11	7.12 ± 0.34	6.12 ± 0.26	−14.1	0.086	ns
Number of Leaves	BARI Hybrid Tomato-08	8.0 ± 0.34	6.0 ± 0.56	−25.0	0.049	*
	BARI Hybrid Tomato-10	7.0 ± 0.40	4.0 ± 0.45	−42.9	0.008	**
	BARI Hybrid Tomato-11	6.0 ± 0.24	5.0 ± 0.52	−16.7	0.186	ns
Leaf RWC (%)	BARI Hybrid Tomato-08	83.0 ± 3.25	75.0 ± 3.40	−9.6	0.164	ns
	BARI Hybrid Tomato-10	79.0 ± 3.30	55.0 ± 3.40	−30.4	0.007	**
	BARI Hybrid Tomato-11	88.0 ± 3.00	72.0 ± 3.00	−18.2	0.020	*
Proline (µmol/g FW)	BARI Hybrid Tomato-08	3.20 ± 0.20	12.50 ± 0.60	+290.6	0.002	**
	BARI Hybrid Tomato-10	3.00 ± 0.30	11.80 ± 0.50	+293.3	<0.001	***
	BARI Hybrid Tomato-11	3.10 ± 0.20	12.20 ± 0.40	+293.5	<0.001	***
Lycopene (mg/g FW)	BARI Hybrid Tomato-08	0.48 ± 0.04	0.41 ± 0.02	−14.6	0.217	ns
	BARI Hybrid Tomato-10	0.44 ± 0.01	0.34 ± 0.03	−22.7	0.067	ns
	BARI Hybrid Tomato-11	0.47 ± 0.01	0.46 ± 0.01	−2.1	0.577	ns
β-Carotene (mg/g FW)	BARI Hybrid Tomato-08	0.19 ± 0.02	0.17 ± 0.01	−10.5	0.449	ns
	BARI Hybrid Tomato-10	0.13 ± 0.02	0.10 ± 0.01	−23.1	0.274	ns
	BARI Hybrid Tomato-11	0.15 ± 0.02	0.12 ± 0.01	−20.7	0.244	ns
Fruit Yield (kg/plant)	BARI Hybrid Tomato-08	1.31 ± 0.03	1.29 ± 0.02	−1.5	0.613	ns
	BARI Hybrid Tomato-10	1.15 ± 0.04	1.00 ± 0.05	−13.0	0.082	ns
	BARI Hybrid Tomato-11	1.44 ± 0.02	1.19 ± 0.03	−17.4	0.004	**

*Significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns: non-significant; Negative % change values indicate reduction under waterlogging; positive values indicate increase (proline only).*

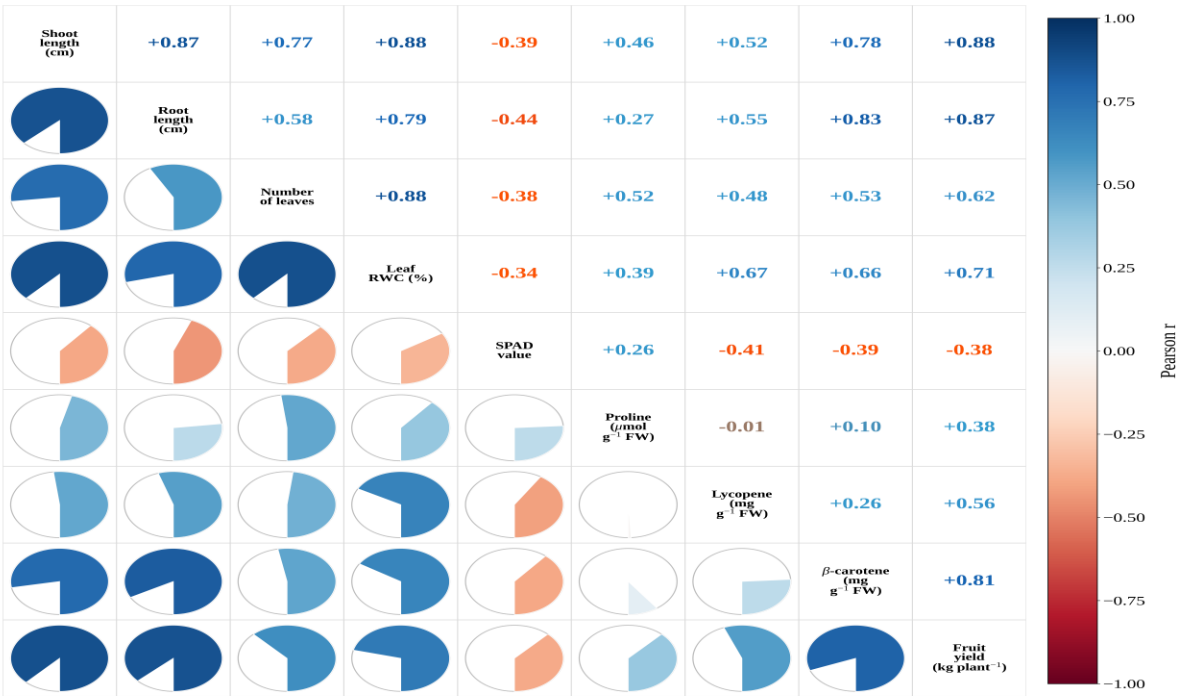

Figure 4. Correlation analysis of all the measured traits in tomato under short-term waterlogging stress.

Effect of Waterlogging on Root Length

Root length was significantly influenced by genotype ($p = 0.003$), waterlogging treatment ($p < 0.001$) and the genotype × treatment interaction ($p = 0.047$; Table 2), demonstrating that the three BARI tomato hybrids differed in their tolerance of three days of root-zone hypoxia. Mean root length was comparable across genotypes under aerated conditions (6.9–7.4 cm; Figure 2B), and genotypic differentiation became evident only after the imposition of stress. BARI Hybrid Tomato-10 was the most sensitive line, with root length declining by 27% relative to its control (5.1 ± 0.2 cm; group b), whereas BARI Hybrid Tomato-08 (6.9 ± 0.1 cm; 93% of control) and BARI Hybrid Tomato-11 (6.1 ± 0.3 cm; 86%) maintained significantly longer roots and were not statistically separated by Tukey's HSD (group a). The continuous distribution of responses is in agreement with the view that waterlogging tolerance in tomato behaves as a quantitative trait, governed by the combined action of cortical aerenchyma formation, ethylene-induced adventitious rooting and ERF-VII–dependent reprogramming of fermentative carbon metabolism (Vidoz et al. 2010; Sasidharan et al. 2017; Loreti and Perata 2020). Direct identification of the mechanism dominating the contrast among the present genotypes will, however, require anatomical and transcriptomic analysis beyond the scope of this work. Within-genotype Welch's tests further showed that only Tomato-10 declined significantly under waterlogging ($p < 0.001$), whereas Tomato-08 ($p = 0.257$) and Tomato-11 ($p = 0.086$) maintained statistically unchanged root length (Table 3).

Effect of Waterlogging on Shoot Length

Shoot length was significantly affected by genotype, treatment and their interaction (all $p < 0.001$; Table 2). Under control conditions the hybrids produced shoots of comparable height (Figure 2A), but waterlogging separated them into three statistically distinct Tukey classes. Here, BARI Hybrid Tomato-08 retained the tallest shoots under stress (12.8 ± 0.1 cm; group a), BARI Hybrid Tomato-11 occupied an intermediate position (10.9 ± 0.4 cm; group b), and BARI Hybrid Tomato-10 was the most affected (7.9 ± 0.3 cm; group c). These values represent retention of 95.1%, 83.7% and 62.8% of the corresponding control means, respectively, placing BARI Hybrid Tomato-08 at the upper end of the response gradient and tomato-10 at the lower end. Within-genotype Welch's tests confirmed this divergence: Tomato-10 declined significantly under waterlogging ($p < 0.001$), Tomato-11 declined to a smaller degree ($p = 0.016$), and Tomato-08 showed no significant change in shoot length ($p = 0.229$; Table 3).

Effect of Waterlogging on Leaf Relative Water Content (RWC)

Leaf RWC was significantly affected by waterlogging across all three genotypes (Treatment effect, $p < 0.001$) and a significant Genotype main effect was also detected ($p = 0.003$), although the genotype × treatment interaction was non-significant ($p = 0.084$; Table 2). Under control conditions, RWC values were broadly comparable across the three genotypes (BARI Hybrid Tomato-08: 83.0 ± 3.3 %; BARI Hybrid Tomato-10: 79.0 ± 3.3 %; BARI Hybrid Tomato-11: 88.0 ± 3.0 %) and were assigned to the same Tukey group (A; Figure 2D). Under waterlogging, BARI Hybrid Tomato-08 maintained 75.0 ± 3.4 % RWC and BARI Hybrid Tomato-11 maintained 72.0 ± 3.0 %, both clustering in Tukey group "a", whereas BARI Hybrid Tomato-10 declined more sharply to 55.0 ± 3.4 % and was placed in a separate group ("b"). The corresponding waterlogging tolerance index values were 90.4 %, 69.6 % and 81.8 % for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10 and BARI Hybrid Tomato-11, respectively. These results indicate that BARI Hybrid Tomato-10 experienced markedly greater loss of leaf water status under three days of waterlogging, while BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 maintained comparably higher RWC and were not statistically separable from each other.

Effect of Waterlogging on Proline Content

Leaf proline accumulation was strongly induced by waterlogging in all three genotypes (Treatment effect, $p < 0.001$), with no significant differences attributable to genotype ($p = 0.540$) or to the genotype

× treatment interaction ($p = 0.820$; Table 2). Under control conditions, proline contents were comparable among the three genotypes (3.2 ± 0.2, 3.0 ± 0.3, and 3.1 ± 0.2 µmol g^{-1} FW for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11, respectively), with all three sharing Tukey group *A*. Under waterlogging stress, proline accumulated to 12.5 ± 0.6, 11.8 ± 0.5, and 12.2 ± 0.4 µmol g^{-1} FW in the same three genotypes, again clustering in a single Tukey group ("*a*"; Figure 2F). This represented an approximately 3.9-fold increase in proline content across all three genotypes. The waterlogging tolerance index falls outside the conventional 0–100 % range because proline accumulates rather than declines under stress; therefore, it should be considered as a stress-response magnitude rather than a tolerance metric. The non-significant genotype and interaction effects indicate that proline accumulation under three days of waterlogging was a generalized stress response rather than a genotype-specific trait. Higher proline accumulation by itself does not indicate greater tolerance; it can equally reflect a higher level of imposed stress.

Effect of Waterlogging on Fruit Lycopene Content

Lycopene content was significantly affected by both genotype ($p = 0.020$) and short-term waterlogging treatment ($p = 0.008$), although the genotype × treatment interaction was non-significant ($p = 0.188$; Table 2). Under control conditions, lycopene contents were comparable across the three genotypes (0.48 ± 0.04, 0.44 ± 0.01, and 0.47 ± 0.01 mg g^{-1} FW for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11, respectively), with all three sharing Tukey group "A". Under waterlogging, BARI Hybrid Tomato-10 declined sharply to 0.34 ± 0.03 mg g^{-1} FW (a 22.7 % reduction) and was placed in a separate Tukey group ("b"), while BARI Hybrid Tomato-08 (0.41 ± 0.02 mg g^{-1} FW) and BARI Hybrid Tomato-11 (0.46 ± 0.01 mg g^{-1} FW) shared a common group ("a") with reductions of only 14.6 % and 2.1 %, respectively (Figure 3A). The corresponding waterlogging tolerance index (WTI) values were 85.4 %, 77.3 %, and 97.9 % for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11, respectively, with BARI Hybrid Tomato-11 showing the highest lycopene WTI value among the three genotypes, although the non-significant genotype × treatment interaction ($p = 0.188$) means this differential should be confirmed in larger panels.

Effect of Waterlogging on Fruit β-Carotene Content

β-carotene content varied significantly among genotypes ($p = 0.004$; Table 2), whereas the treatment effect was only marginal ($p = 0.059$) and the genotype × treatment interaction was non-significant ($p = 0.929$). BARI Hybrid Tomato-08 maintained the highest β-carotene content under both control (0.19 ± 0.02 mg g^{-1} FW) and waterlogged conditions (0.17 ± 0.01 mg g^{-1} FW), followed by BARI Hybrid Tomato-11 (0.15 ± 0.02 and 0.12 ± 0.01 mg g^{-1} FW) and BARI Hybrid Tomato-10 (0.13 ± 0.02 and 0.10 ± 0.01 mg g^{-1} FW). Tukey's HSD grouped BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 together under both treatments ("A" and "a"), while BARI Hybrid Tomato-10 separated as "B" and "b" (Figure 3B). Mean reductions from control to waterlogged conditions were modest and comparable across genotypes (10.5 %, 23.1 %, and 20.0 % for BARI Hybrid Tomato-08, BARI Hybrid Tomato-10, and BARI Hybrid Tomato-11, respectively), consistent with the non-significant interaction. BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 maintained statistically comparable β-carotene content under waterlogging, with BARI Hybrid Tomato-08 showing the highest WTI value (89.5%) (Figure 1).

Effect of Waterlogging on Fruit Yield

Fruit yield was significantly affected by genotype ($p < 0.001$), waterlogging treatment ($p < 0.001$), and their interaction ($p = 0.016$; Table 2). The significant G × T interaction indicates that the three genotypes responded differently to waterlogging in terms of fruit yield. Under control conditions, the three genotypes were placed in three distinct Tukey groups, with BARI Hybrid Tomato-11 producing the highest fruit yield (1.44 ± 0.02 kg $plant^{-1}$, group "A"), followed by BARI Hybrid Tomato-08 (1.31 ± 0.03 kg $plant^{-1}$, group "B") and BARI Hybrid Tomato-10 (1.15 ± 0.04 kg $plant^{-1}$, group "C"). Under waterlogging, this ranking shifted: BARI Hybrid Tomato-08 (1.29 ± 0.02 kg $plant^{-1}$) and BARI Hybrid

Tomato-11 (1.19 ± 0.03 kg plant^{-1}) were no longer separable and shared a common group ("a"), while BARI Hybrid Tomato-10 dropped to 1.00 ± 0.05 kg plant^{-1} and remained in a separate group ("b") (Figure 3C). Yield reductions from control to waterlogged conditions were 1.5 % in BARI Hybrid Tomato-08, 13.0 % in BARI Hybrid Tomato-10, and 17.4 % in BARI Hybrid Tomato-11, with corresponding waterlogging tolerance index (WTI) values of 98.5 %, 87.0 %, and 82.6 %, respectively (Figure 1). Under waterlogging, BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 produced statistically comparable yields (group "a"), with BARI Hybrid Tomato-08 showing the highest WTI value (98.5 %) and the smallest proportional decline. BARI Hybrid Tomato-11 showed the largest proportional decline under stress, while BARI Hybrid Tomato-10 produced the lowest yield under both control and stress conditions. Within-genotype Welch's tests showed that yield declined significantly under waterlogging only in Tomato-11 (p = 0.004), while Tomato-08 (p = 0.613) and Tomato-10 (p = 0.082) did not show statistically significant within-genotype reductions (Table 3).

Correlation analysis

Pearson correlation coefficients (r) were computed pairwise among the measured traits within the waterlogged treatment (n = 9; df = 7; critical r = ±0.666 at p = 0.05). The full pairwise correlation matrix is presented in Figure 4. Twelve of the 36 unique pairwise correlations were statistically significant at p < 0.05, all positive except for SPAD, which showed weak, non-significant negative associations with most other traits.

The strongest correlations occurred within a coherent block of morphological, water-status and yield traits. Shoot length correlated positively with root length (r = +0.87, p = 0.002), number of leaves (r = +0.77, p = 0.015), leaf RWC (r = +0.86, p = 0.003), β-carotene (r = +0.78, p = 0.014) and fruit yield (r = +0.88, p = 0.002). Root length correlated with leaf RWC (r = +0.79, p = 0.011), β-carotene (r = +0.83, p = 0.006) and fruit yield (r = +0.87, p = 0.002). Leaf RWC also correlated with number of leaves (r = +0.80, p = 0.010), lycopene (r = +0.67, p = 0.050) and fruit yield (r = +0.71, p = 0.031). β-carotene correlated with fruit yield (r = +0.81, p = 0.008). Four correlations remained significant under Bonferroni correction for 36 tests: shoot × root, shoot × yield, root × yield and shoot × leaf RWC.

In contrast, SPAD showed weak, consistently negative correlations with other traits (all |r| < 0.67, none significant). Proline was uncorrelated with all other traits (all |r| ≤ 0.52, all p > 0.05). Lycopene was significantly correlated only with leaf RWC (r = +0.67, p = 0.050).

Discussion

In this study, the two-way factorial ANOVA results showed a significant Genotype × Treatment interaction for shoot length, root length, and fruit yield. Of the nine traits studied, these three showed genotype-specific responses to short-term waterlogging stress. The remaining traits responded uniformly across genotypes under stress. Under short-term waterlogging, the genotypes fell into three statistically distinct Tukey groups, with BARI Hybrid Tomato-08 maintaining the tallest shoots followed by BARI Hybrid Tomato-11 and BARI Hybrid Tomato-10. The observed differential response in aerial growth is consistent with the findings of Yin et al. (2023) and Umićević et al. (2024). They reported that shoot elongation under flooding has served as an integrative indicator of waterlogging tolerance among genetically diverse material. Sustained shoot growth under root-zone hypoxia depends on several processes working in concert above as well as within the root system: longitudinal oxygen transport through cortical aerenchyma, ethylene-mediated regulation of internode expansion, and reprogramming of fermentative carbon metabolism that preserves the ATP supply needed for cell division when mitochondrial respiration is restricted (Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015).

According to the results of this study, while all genotypes were affected by waterlogging in chlorophyll content (SPAD value), proline, RWC, and carotenoid content, the non-significant G × T interactions for these traits imply that BARI Hybrid Tomato-08 did not respond in a way that was statistically distinguishable from BARI Hybrid Tomato-11. The uniform rise in proline among all three genotypes looks more like a generalized osmotic adjustment than a tolerance-specific mechanism (Szabados & Savouré, 2010). The broadly comparable carotenoid responses probably reflect the brief, relatively mild nature of the imposed stress. Moreover, hypoxia is known to downregulate carotenoid biosynthesis genes such as PSY and LCYB (Giuliano, 2017), but three days of flooding may simply be too short a window for genotype-level differentiation.

Fruit lycopene declined under waterlogging, consistent with evidence that root-zone hypoxia and associated oxidative stress can disrupt carotenoid biosynthesis and fruit-quality development in tomato (Mohanty et al., 2020; Anee et al., 2025). Lycopene accumulation depends strongly on carotenoid-biosynthetic flux through phytoene synthase and phytoene desaturase and is sensitive to carbon supply and plastid redox status (Giuliano, 2017; Zhou et al., 2022). Under hypoxic root conditions, reduced photosynthetic activity and assimilate supply can limit isoprenoid and carotenoid biosynthesis, contributing to lower pigment accumulation (Horchani et al., 2010; Ide et al., 2022). BARI Hybrid Tomato-11 retained the highest proportion of lycopene under waterlogging, but the G × T interaction was not significant; therefore, lycopene stability should be treated as a promising quality observation requiring confirmation in larger genotype panels and field trials.

The β-carotene response differed from the lycopene response in an interesting way. Here, genotype rather than waterlogging itself was the main driver of variation, and the three-day treatment produced only a marginal overall reduction. This result is consistent with Anee et al. (2025), who reported that waterlogging caused reductions in carotenoids but with effects that varied considerably with genetic background, and with Mohanty et al. (2020) who reported that short-term flooding altered total carotenoid content rather modestly compared with the reductions in chlorophyll and biomass. We found that BARI Hybrid Tomato-08 maintained the highest β-carotene content across both treatments. This result is aligned with Yin et al. (2023) who reported genotype-level differences in fruit pigment under waterlogging persisted but did not reverse under stress. Moreover, Umićević et al. (2024) concluded that genotype modulates fruit-quality traits during repeated flooding in tomato. In our study, the G × T interaction for β-carotene was not significant, meaning the three BARI genotypes were affected by waterlogging to a similar extent; the differences seen between them simply reflect their natural β-carotene levels rather than any genotype-specific tolerance to the stress. BARI Hybrid Tomato-08 had the highest fruit β-carotene content under control conditions. All three genotypes showed similar β-carotene reductions under waterlogging where BARI Hybrid Tomato-08 also remained the highest of the three after stress.

The Pearson correlation analysis revealed a strongly coordinated response among morphological, physiological, and biochemical traits of tomato under short-term waterlogging stress. The strong positive associations among shoot length, root length, leaf number, and leaf relative water content (RWC), and their collective coupling with fruit yield, indicate that vegetative vigour and tissue hydration are the primary determinants of reproductive success under hypoxic conditions. These findings are in agreement with Umićević et al. (2024) and Bhatt et al. (2015), who reported that waterlogging-induced oxygen deprivation simultaneously impairs root function, canopy expansion, and assimilate supply in tomato, and with Jackson (2008), who linked flooding-induced reductions in root-derived gibberellins to coordinated declines in shoot growth. The emergence of leaf RWC and root length as the strongest yield predictors aligns with Zhou et al. (2022) and Soltys-Kalina et al. (2016), who identified tissue hydration and root architecture as the most reliable single-trait indicators of tolerance to flooding and related abiotic stresses across crop species. The inverse correlation of SPAD value with growth and yield variables, although counter-intuitive, likely reflects the well-known concentration effect, whereby restricted leaf expansion elevates chlorophyll density per unit area without enhancing photosynthetic capacity — a pattern previously documented by Li et al. (2023) in winter rapeseed and Zeng et al. (2021) in peanut under waterlogging, and one that cautions against the use of SPAD as a stand-alone tolerance indicator.

The carotenoid profile of fruits provided a complementary quality-oriented dimension to the tolerance response. The strong positive correlation between lycopene and β-carotene, and the parallel positive associations of both pigments with shoot length, root length, leaf RWC, and fruit yield, reflect the shared methylerythritol phosphate origin of these pigments and the tight metabolic coupling between lycopene cyclisation and β-carotene formation, as detailed by D'Ambrosio et al. (2004). These results align with the findings of Kössler et al. (2021), who showed that genotypes maintaining higher carotenoid biosynthesis via lycopene β-cyclase expression also retain greater biomass and improved metabolic performance, indicating that whole-plant tolerance mechanisms translate into preserved nutritional value of the harvest. In contrast, proline showed weak correlations with growth, yield, and carotenoid traits, consistent with Spormann et al. (2023), who argued that proline accumulation often signals the magnitude of perceived stress rather than the plant's capacity to cope with it, and therefore should not serve as a stand-alone selection criterion. Taken together, these correlations identify leaf RWC and root length as the most informative phenotyping targets for waterlogging tolerance in tomato, with fruit carotenoid content offering a useful quality-linked marker — a multi-trait framework increasingly relevant as flooding events intensify under climate change (Pucciariello & Perata, 2024).

Limitations of this study

This study has several limitations. First, the number of genotypes studied was limited, which may restrict the generalizability of the findings to the wider tomato germplasm. Second, the experiment was not conducted under field conditions, and the results may differ in the field due to variations in environmental factors. Third, soil oxygen concentration and redox potential were not quantified during the waterlogging treatment. In addition, the waterlogging treatment lasted only three days; longer waterlogging stress may produce different physiological responses and greater yield losses. Finally, the data presented here are from a single growing season, so genotype × year interactions could not be assessed. Future research could incorporate more genotypes, longer waterlogging durations (5 to 10 days), multi-season field trials, detailed root imaging, in situ measurement of soil O_2 and redox potential, and targeted molecular and biochemical assays to strengthen the evaluation of waterlogging tolerance in tomato.

Conclusion

This study provides a preliminary characterization of waterlogging responses among three BARI Hybrid Tomato genotypes under short-term stress. Two-way factorial ANOVA identified shoot length, root length and fruit yield as the only traits with a significant genotype × treatment interaction, making them the most informative for distinguishing genotype-specific responses in this study. For all three of these traits, BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 maintained significantly higher values than BARI Hybrid Tomato-10 under waterlogging, while not differing significantly from each other for root length or fruit yield; for shoot length specifically, BARI Hybrid Tomato-08 retained slightly more growth than BARI Hybrid Tomato-11. For the remaining traits such as chlorophyll content, leaf number, RWC, proline, lycopene and β-carotene — the genotype × treatment interaction was non-significant, indicating that these traits did not respond differentially to waterlogging among the three genotypes. Across both morphological and biochemical parameters, BARI Hybrid Tomato-10 was consistently the most adversely affected genotype. Based on this preliminary screen, BARI Hybrid Tomato-08 and BARI Hybrid Tomato-11 are recommended for further evaluation under field conditions, longer waterlogging durations and additional growth stages, while BARI Hybrid Tomato-10 represents a sensitive reference line.

Authorship contribution:

Khadiza Khatun: Conceptualization, project administration, funding acquisition, supervision, validation, review and editing. **Md. Mainul Islam Rashad:** Data curation, methodology, formal analysis, investigation, software, visualization, writing – original draft, review and editing. **Md Shafikur Rahman:** Conceptualization, review and editing, data curation. **Asmaul Husna:** Review and editing. **Md. Rafiqul Islam:** Conceptualization, writing – review and editing. **Ashish Biswas:** Data curation, writing – review and editing. **Sadhon Kumar Acharjee:** Data curation, review and editing, resources.

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References

Ábrahám, E., Hourton-Cabassa, C., Erdei, L., & Szabados, L. (2010). Methods for determination of proline in plants. In R. Sunkar (Ed.), *Plant stress tolerance. Methods in Molecular Biology* (Vol. 639, pp. 317–331). Humana Press. https://doi.org/10.1007/978-1-60761-702-0_20

Ahmed, S., Akter, M. A., & Hasanuzzaman, M. (2020). Morphological and physiological responses of tomato under waterlogging stress. *Plant Physiology Reports*, 25(2), 217–226.

Anee, T. I., Rachman, R. R., Ziqi, Z., & Suzuki, N. (2025). A combination of salt stress and waterlogging provides protection to tomato plants against the negative effects of waterlogging individually applied. Physiologia Plantarum, 177(1), e70116. https://doi.org/10.1111/ppl.70116

Bailey-Serres, J., & Voesenek, L. A. (2008). Flooding stress: acclimations and genetic diversity. *Annual Review of Plant Biology*, 59, 313–339.

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2017). The role of root exudates in plant–soil interactions. *Annual Review of Plant Biology*, 58, 233–266.

Barrs, H. D., & Weatherley, P. E. (1962). A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Australian Journal of Biological Sciences*, 15(3), 413–428.

Bhatt, R. M., Upreti, K. K., Divya, M. H., Bhat, S., Pavithra, C. B., & Sadashiva, A. T. (2015). Interspecific grafting to enhance physiological resilience to flooding stress in tomato (Solanum lycopersicum L.). Scientia Horticulturae, 182, 8–17. https://doi.org/10.1016/j.scienta.2014.10.043

Colmer, T. D., & Voesenek, L. A. C. J. (2009). Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology*, 36(8), 665–681.

D'Ambrosio, C., Giorio, G., Marino, I., Merendino, A., Petrozza, A., Salfi, L., Stigliani, A. L., & Cellini, F. (2004). Virtually complete conversion of lycopene into β-carotene in fruits of tomato plants transformed with the tomato lycopene β-cyclase (tlcy-b) cDNA. Plant Science, 166(1), 207–214. https://doi.org/10.1016/j.plantsci.2003.09.015

FAO. (2022). FAOSTAT: Crops and livestock products. Food and Agriculture Organization of the United Nations. Retrieved from https://www.fao.org/faostat

Ferdous, Z., Datta, A., & Anwar, M. (2017). Plastic mulch and indigenous microorganism effects on yield and yield components of cauliflower and tomato in inland and coastal regions of Bangladesh. *Journal of Crop Improvement*, *31*(3), 261–279. https://doi.org/10.1080/15427528.2017.1293578.

Fish, W. W., Perkins-Veazie, P., & Collins, J. K. (2002). A quantitative assay for lycopene that utilizes reduced volumes of organic solvents. Journal of Food Composition and Analysis, 15(3), 309–317.

Fraser, P. D., Truesdale, M. R., Bird, C. R., Schuch, W., & Bramley, P. M. (2000). Carotenoid biosynthesis during tomato fruit development. *Plant Physiology*, 105(1), 405–413.

Giuliano, G. (2017). Provitamin A biofortification of crop plants: a gold rush with many miners. *Current Opinion in Biotechnology*, 44, 169–180.

Hagage, M., Abdulaziz, A. M., Elbeih, S. F., & Hewaidy, A. G. A. (2024). Monitoring soil salinization and waterlogging in the northeastern Nile Delta linked to shallow saline groundwater and irrigation water quality. Scientific Reports, 14(1), 27838. https://doi.org/10.1038/s41598-024-77954-x

Horchani, F., Stammitti-Bert, L., Baldet, P., Brouquisse, R., Rolin, D., Aschi-Smiti, S., Raymond, P., & Gallusci, P. (2010). Effect of prolonged root hypoxia on the antioxidant content of tomato fruit. *Plant Science*, *179*(3), 209–218. https://doi.org/10.1016/j.plantsci.2010.05.003

Ide, R., Ichiki, A., Suzuki, T., & Jitsuyama, Y. (2022). Analysis of yield reduction factors in processing tomatoes under waterlogging conditions. *Scientia Horticulturae*, 295, 110840.

Jackson, M. B. (2008). Waterlogging effects in tomato. In M. Razdan & A. K. Mattoo (Eds.), Genetic improvement of Solanaceous crops, Volume 2: Tomato (pp. 73–95). Science Publishers.

Khan, M. Z., & Shoumik, B. A. A. (2022). Land degradation neutrality concerns in Bangladesh. Soil Security. https://doi.org/10.1016/j.soisec.2022.100075

Kössler, S., Armarego-Marriott, T., Tarkowská, D., Turečková, V., Agrawal, S., Mi, J., de Souza, L. P., Schöttler, M. A., Schadach, A., Fröhlich, A., Bock, R., Al-Babili, S., Ruf, S., Sampathkumar, A., & Moreno, J. C. (2021). Lycopene β-cyclase expression influences plant physiology, development, and metabolism in tobacco plants. Journal of Experimental Botany, 72(7), 2544–2569. https://doi.org/10.1093/jxb/erab029

Lichtenthaler, H. K. (1987). Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. *Methods in enzymology*. Vol. 148. Academic Press, 350-382.

Li, L., Zhang, L., Tang, J., Xing, H., Zhao, L., Jie, H., & Jie, Y. (2023). Waterlogging increases greenhouse gas release and decreases yield in winter rapeseed (Brassica napus L.) seedlings. Scientific Reports, 13(1), 18673. https://doi.org/10.1038/s41598-023-46156-2

Loreti, E., & Perata, P. (2020). The many facets of hypoxia in plants. Plants, 9(6), 745. https://doi.org/10.3390/plants9060745

Mohanty. A., Panda, R. K., Rout, G. R., Muduli K. C. and Tripathy. P. (2020). Effect of Short Term Waterlogging on Plant Morphology, Chlorophyll and Carotenoid Content of Tomato (*Solanum lycopersicum* L. Mill) during Vegetative Stage. International *Journal of Current Microbiology and Applied Sciences*, 9(7): 920-935. https://doi: https://doi.org/10.20546/ijcmas.2020.907.107

Mondal, M. M. A., Imam, M. H., & Razzaque, A. H. M. (2011). Effect of seasonal seeds on growth and yield of tomato genotypes. *International Journal of Experimental Agriculture*, 2(1), 12-16.

Pucciariello, C., & Perata, P. (2024). Could flooding undermine progress in building climate-resilient crops? Trends in Plant Science, 29(11), 1245–1256. https://doi.org/10.1016/j.tplants.2024.07.011

Rathore, A.C., Mehta, H., Jayaprakash, J. et al. Modified plant architecture integrated with liquid fertilizers improves fruit productivity and quality of tomato in North West Himalaya, India. Sci Rep 11, 18664 (2021). https://doi.org/10.1038/s41598-021-98209-z

Sasidharan, R., Bailey-Serres, J., Ashikari, M., Atwell, B.J., Colmer, T.D., Fagerstedt, K., Fukao, T., Geigenberger, P., Hebelstrup, K.H., Hill, R.D., Holdsworth, M.J., Ismail, A.M., Licausi, F., Mustroph, A., Nakazono, M., Pedersen, O., Perata, P., Sauter, M., Shih, M.-C., Sorrell, B.K., Striker, G.G., van Dongen, J.T., Whelan, J., Xiao, S., Visser, E.J.W., & Voesenek, L.A.C.J. (2017). Community recommendations on terminology and procedures used in flooding and low oxygen stress research. New Phytologist, 214(4), 1403–1407. https://doi.org/10.1111/nph.14519

Soltys-Kalina, D., Plich, J., Strzelczyk-Żyta, D., Śliwka, J., & Marczewski, W. (2016). The effect of drought stress on the leaf relative water content and tuber yield of a half-sib family of 'Katahdin'-derived potato cultivars. Breeding Science, 66(2), 328–331. https://doi.org/10.1270/jsbbs.66.328

Spormann, S., Nadais, P., Sousa, F., Pinto, M., Martins, M., Sousa, B., Fidalgo, F., & Soares, C. (2023). Accumulation of proline in plants under contaminated soils—Are we on the same page? Antioxidants, 12(3), 666. https://doi.org/10.3390/antiox12030666

Umićević, S., Kukavica, B., Maksimović, I., et al. (2024). Stress response in tomato as influenced by repeated waterlogging. Frontiers in Plant Science, 15, 1331281. https://doi.org/10.3389/fpls.2024.1331281

Vidoz, M. L., Loreti, E., Mensuali, A., Alpi, A., & Perata, P. (2010). Hormonal interplay during adventitious root formation in flooded tomato plants. The Plant Journal, 63, 551–562.

Voesenek, L.A.C.J. & Bailey-Serres, J. (2015). Flood adaptive traits and processes: an overview. *New Phytologist* 206, 57–73.

Szabados, L., & Savouré, A. (2010). Proline: a multifunctional amino acid. *Trends in Plant Science*, 15(2), 89–97.

Yin, J., Niu, L., Li, Y., Song, X., Ottosen, C.-O., Wu, Z., Jiang, F., & Zhou, R. (2023). The effects of waterlogging stress on plant morphology, leaf physiology and fruit yield in six tomato genotypes at anthesis stage. *Vegetable Research*, 3, 31. https://doi.org/10.48130/VR-2023-0031

Zaman, M. M., Anawarul Huq, A. S. M., & Chowdhury, M. J. A. (2006). Production potentiality of summer tomato in Jamalpur region. International Journal of Sustainable *Crop Production*, 1(2), 12–15.

Zechmeister, L., LeRosen, A.L., Went, F.W., and Pauling, L. (1941). Prolycopene, a naturally occurring stereoisomer of lycopene. Proceedings of the National Academy of Sciences, 27, 468–474.

Zeng, R., Chen, T., Wang, X., Cao, J., Li, X., Xu, X., Chen, L., Wang, Q., & Zhang, J. (2021). Physiological and expressional regulation on photosynthesis, starch and sucrose metabolism response to waterlogging stress in peanut. Frontiers in Plant Science, 12, 601771. https://doi.org/10.3389/fpls.2021.601771

Zhou, R., Jiang, F., Yu, X., Abdelhakim, L., Li, X., Rosenqvist, E., Liu, F., & Wu, Z. (2022). Dominant and priming role of waterlogging in tomato at e[CO_2] by multivariate analysis. International Journal of Molecular Sciences, 23(20), 12121. https://doi.org/10.3390/ijms232012121