PLANT SCIENCE TODAY
Vol 12(sp1): 1-11
https://doi.org/10.14719/pst.7929

eISSN 2348-1900

RESEARCH ARTICLE

Waterlogging induced morpho-physiological and biochemical changes in maize (*Zea mays* L.) seedlings

M Tejashwi[1], M P Mandal[1], S Nahakpam[1*], R Kesari[2], T Ranjan[2] & S S Mandal[3]

[1]Department of Plant Physiology and Biochemistry, Bihar Agricultural University, Sabour 813 210, Bhagalpur, Bihar, India
[2]Department of Molecular Biology and Genetic Engineering, Bihar Agricultural University, Sabour 813 210, Bhagalpur, Bihar, India
[3]Department of Plant Breeding and Genetics, Bihar Agricultural University, Sabour 813 210,, Bhagalpur, Bihar, India

*Correspondence email - nichsareeta@gmail.com

Received: 25 February 2025; Accepted: 14 August 2025; Available online: Version 1.0: 16 October 2025

Cite this article: Tejashwi M, Mandal MP, Nahakpam S, Kesari R, Ranjan T, Mandal SS. Waterlogging induced morpho-physiological and biochemical changes in maize (*Zea mays* L.) seedlings. Plant Science Today. 2025; 12(sp1): 1-11. https://doi.org/10.14719/pst.7929

Abstract

This study investigated the effects of waterlogging on two maize genotypes (BML6 and BML7) at two distinct seedling stages asSet 1 and Set 2 (11 - 17 days and 21 - 27 days). Waterlogging significantly impacted plant growth, leading to reduced leaf area (LA) in both genotypes. The tolerant genotype BML7 maintained a significantly larger LA (113 cm^2) compared to the sensitive genotype BML6 (92.09 cm^2) by the 27th day of stress exposure. Across both developmental stages, leaf senescence was more pronounced in BML6, with a 50 % leaf death rate, compared to 37 % in BML7. Waterlogging stress adversely affected plant growth, resulting in a reduction in final biomass by 20 % in BML6 and 15 % in BML7. Additionally, waterlogging led to a significant decline in relative water content (RWC) (by approximately 15 %) and chlorophyll content (by 20 %) in both genotypes. Biochemical assessments indicated marked changes, with total carbohydrate content decreasing by 15 % in BML6 and 10 % in BML7.Hydrogen peroxide (H_2O_2) levels increased threefold at the late seedling stage, while peroxidase (POD) activity increased by 30 % in BML7 under waterlogged conditions, suggesting a stronger antioxidant response in the tolerant genotype. These findings demonstrate significant genotypic variation in waterlogging tolerance among maize cultivars. Further research is crucial to identify key physiological, biochemical and morphological traits associated with waterlogging stress tolerance in maize. Characterizing these traits will facilitate the development of maize cultivars with enhanced resilience to waterlogging stress, a critical adaptation in light of the increasing frequency and intensity of flooding events driven by climate change.

Keywords: antioxidative enzymes; chlorophyll; leaf senescence; maize; relative water content; waterlogging

Introduction

Waterlogging, recognized as a major constraint on agricultural productivity, poses a significant threat to crop growth and yield, particularly for crops like maize (1). This condition arises when the soil water content surpasses field capacity by at least 20 %, resulting in the accumulation of standing water on the soil surface (2). The detrimental effects of waterlogging creates anaerobic conditions disrupting nutrient cycling, reduce biodiversity and impacting the sustainability of agricultural lands and natural ecosystems. It disrupts plant growth, reduces productivity and alters the distribution of plant species. Several factors contribute to waterlogging, including excessive precipitation, inadequate drainage systems, faulty irrigation practices, unpredictable rainfall events, high water tables and heavy soil textures. Waterlogging primarily impacts plant growth by reducing oxygen availability in the soil, a condition known as hypoxia (3). Prolonged waterlogging can lead to anoxia, the complete absence of oxygen because excess water impedes oxygen diffusion in the soil (4).

Additionally, aerobic microorganisms in the rhizosphere consume oxygen, further reducing its availability (5). Oxygen concentrations vary within plant tissues, ranging from 1 – 7 % in well-aerated organs. Hypoxia occurs when oxygen levels are insufficient for efficient ATP production in mitochondria, disrupting cellular respiration (6). *Z. mays* L. is a globally vital crop used for food, feed and industry, with demand rising by 45 % between 2000 and 2020 (7) due to population growth, increased animal product consumption and biofuel use. However, waterlogging a major stress caused by excessive soil moisture poses a critical threat, potentially reducing yields by over 50 % (1) and its impact is intensifying due to more frequent extreme weather events linked to climate change (8). These factors underscore the urgent need for developing waterlogging tolerant maize varieties. Additionally, implementing sustainable water management practices is essential to ensure food security and agricultural sustainability in the face of growing global demand for this vital crop. Waterlogging, caused by intermittent flooding, prolonged rainfall, improper drainage or a high groundwater table, is a major abiotic stress limiting maize production in Asia and globally. Moreover, South and Southeast Asian countries including India alone, is frequently affected by waterlogging with an approximate of more than 18 % of the total maize growing area, which dominates 25 – 30 % of annual production losses (9, 10).

Plant responses to waterlogging often manifest as significant morphological changes. These alterations are crucial for crop adaptation to challenging environmental conditions and ultimately determine yield. Plant growth and development involve intricate interactions between the roots and shoot systems, influencing resource allocation. Waterlogging can induce leaf chlorosis, necrosis, defoliation, growth cessation and even plant death (10). Reduced growth, particularly root elongation and inhibited hypocotyl pigmentation in soybean seedlings under waterlogging stress, was observed (11, 12). In maize, waterlogging can reduce stomatal conductance, leaf yellowing, inhibit root growth, alter root and shoot morphology, leaf senescence and the development of adventitious roots (13). Key growth parameters, such as plant height, root length and leaf number are intricately linked to physiological processes that concurrently disrupted by waterlogging stress, leading to significant reductions in plant height, particularly in susceptible maize genotypes (14-16). The severity and duration of waterlogging stress during critical growth stages significantly impact final yield (17, 18).

Waterlogging stress during early growth can accelerate plant mortality by driving physiological processes towards senescence, ultimately reducing yield (12, 19-21). This is often accompanied by chlorophyll degradation, as chlorophyll, the primary photosynthetic pigment is sensitive to abiotic stresses. Reduced chlorophyll content has been observed in maize (9, 13), field bean (22) and tomato (23) under waterlogging conditions. Furthermore, waterlogging significantly impacts plant water relations, decreasing RWC. Maintaining higher RWC is crucial for plant survival under stress conditions. Earlier studies have shown that genotypes with higher RWC exhibit improved performance under flooding stress in common bean (24) and rice (25).

Waterlogging stress induces oxidative stress in plants by generating reactive oxygen species (ROS) such as H_2O_2. Plants possess antioxidant defence mechanisms, including low molecular weight antioxidants and enzymes like superoxide dismutase (SOD), catalase (CAT) and PODs , to mitigate oxidative damage. H_2O_2, a key ROS, can act as a signalling molecule, but its excessive accumulation can be detrimental (15). Plants adapted to waterlogging may employ strategies such as increased sugar availability and enhanced antioxidant defence mechanisms to cope with oxidative stress (26). H_2O_2 is a crucial component of ROS-mediated signal transduction because it can penetrate cell membranes (27). Waterlogging can alter H_2O_2 production and its levels are tightly regulated by enzymes like CAT and PODs (28, 29). PODs, a group of enzymes that utilize H_2O_2 as an electron acceptor, play a crucial role in antioxidant defence. Increased POD activity has been reported in response to various abiotic stresses, including drought and waterlogging (14, 30).

While some reports indicate that crops can tolerate waterlogging stress through various plant growth mechanisms, these responses are often limited. Consequently, they frequently fail to result in significant yield improvements. Maize is susceptible to waterlogging, especially during the seedling and early vegetative stages. This stress alters several plants morphological and physio-biochemical attributes, directly or indirectly impacting yield. Furthermore, waterlogging is a major constraint in Bihar, affecting a substantial area of agricultural land annually. Therefore, understanding the morphological and physiological traits that confer waterlogging tolerance in maize is crucial. This knowledge will facilitate in identifying and developing of genotypes or hybrids that can maintain high yields under temporarily waterlogged conditions.

Materials and Methods

A pot experiment was conducted using two maize inbred genotypes BML6 (susceptible) and BML7 (moderately tolerant) obtained from Acharya N. G. Ranga Agricultural University (ANGRAU), Guntur to assess their response to waterlogging stress during the seedling stage. A completely randomized design (CRD) was employed with five numbers of replications. Waterlogging stress was imposed by maintaining 3 - 5 cm water above the soil at two sets i.e. Set 1 depicted by continuous waterlogging treatments 11 - 17 day of growth (DAG) and Set 2 waterlogging from 21 - 27 DAG and data were recorded at 2 day interval for each set as T_0, T_1, T_2 and T_3 respectively.

Plant height and root length were measured using cm scale for one representative plant in each pot with 5 replications at respective stages.

Physiological parameters such as root: shoot ratio, LA, RWC, total chlorophyll and chlorophyll stability index (CSI) were measured.

LA was calculated by using the formula:

LA = l x b x k,

Where, l = length of the leaf

b = breadth of the leaf

k =coefficient value that had been derived

RWC was calculated using formula:

$$\text{RWC (\%)} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Turgid weight} - \text{Dry weight}} \times 100$$

CSI was calculated using the formula:

$$\text{CSI (\%)} = \frac{\text{Total chlorophyll content (heated)}}{\text{Total chlorophyll content (control)}} \times 100$$

Chlorophyll content was determined in a fully expanded leaf from the main tiller and estimated (31).

The expression level of H_2O_2 and POD enzyme activity were estimated (32). The fresh leaf tissue (200 mg) was homogenized in 2 mL of 10 mM potassium phosphate buffer (pH 7.0) in ice-cold condition. The homogenate was centrifuged at 10000xg for 20 min at 4 ºC and the supernatant was used for the assay. Estimated H_2O_2 content was expressed in terms of μ moles g^{-1} fr wt. POD activity was assayed by homogenizing about 200 mg of leaf tissue in 5 mL of 60 mM phosphate buffer (pH 6.0) using a chilled mortar and pestle at 4 ºC. The homogenates were centrifuged at 22000g for 10 min and supernatant were used for enzyme assay. The assay mixture in a final volume of 2 mL contained 50 μL enzyme, 200 μL guaiacol and 50 μL H_2O_2 in 1.7 mL of buffer. The increase in absorbance was measured at 470 nm (extinction coefficient 26.6 mM^{-1} cm^{-1}). Enzyme -specific activity is expressed as μmoL H_2O_2 reduced mg^{-1} protein min^{-1}.

Total carbohydrate content was also determined (33). 200 mg of fresh leaf was taken in test tubes and 5 mL of 2.5 N HCl was added on it and incubated in water bath for 3 hr to hydrolyze the sugars. After cooling at room temperature, sufficient quantity of solid sodium carbonate was added until the effervescence ceases. After filtration, 0.2 mL of sample was taken in separate test tube and 0.5 mL of phenol solution was added and shook well. Then, 2.5 mL of sulphuric acid 96 % was added. The mixture was mixed well and left at room temperature to cool. The absorbance of the developed colour was recorded at 490 nm.

Statistical analysis

Means of five replications were taken for each treatment and statistical significance was calculated using three-way Analysis of variance (ANOVA).

Results and Discussion

Morphological changes

Waterlogging significantly reduced plant height in both BML6 and BML7 maize in both the growth stages (Set 1 and Set 2) compared to the control (Table 1). This reduction was more pronounced in the susceptible BML6 genotype and intensified with the duration of waterlogging stress. While the interaction between genotype, waterlogging and growth stage did not significantly influence plant height, the findings demonstrate the detrimental impact of waterlogging on growth. Waterlogging restricts oxygen diffusion to plant roots, creating hypoxic or anoxic conditions. This oxygen deficiency inhibits aerobic respiration, the primary pathway for ATP production in plant cells. Consequently, reduced energy production limits vital processes such as cell division, elongation and the synthesizing essential biomolecules. This energy deficit ultimately translates into reduced plant growth, including a significant decrease in plant height. This phenomenon has been observed across various crops including soybean, field beans, peanut etc. (16, 22 & 24). Furthermore, waterlogging induces hormonal imbalances, particularly elevated ethylene levels, which accelerate senescence and inhibit growth. Concurrently, anaerobic conditions lead to the accumulation of harmful byproducts, such as acetaldehyde, which compounds stress-related damage and reduces overall plant vigor (34). The present study also highlighted morphological differences in leaf senescence between control and waterlogged conditions for both genotypes at the seedling stage in Set 1 and Set 2 (Fig. 1). This also further illustrated the early onset of senescence in BML6 under waterlogging stress, characterized by yellowing and wilting leaves, whereas BML7 displayed a more resilient leaf appearance, maintaining vigor under the same conditions.

Despite the reduction in plant height, root length increased over time under waterlogged conditions compared to the control in both BML6 and BML7 genotypes at both growth stage, reaching 28.20 cm and 29.60 cm respectively, on day 27 (Set 2), surpassing the initial measurements of 9.88 cm and 9.38 cm on day 11 (Set 1). The interactions study revealed the maximum root length in BML7 with 20.70 cm at control and 29.60 cm under waterlogging conditions on 27th day. Previous studies reported substantial reductions in root length, with maize experiencing up to a 50 % decrease and soybean showing a 38 % reduction (12). These discrepancies may stem from factors such as variations in maize genotypes, differences in experimental conditions (e.g., duration and severity of waterlogging, soil type) and the specific focus and methodologies employed in the current study compared to previous research. To reconcile these findings and gain a more comprehensive understanding of the impact of waterlogging on root growth across different crops, further investigation is required, including method comparisons and analyses of genotypic variations.

Table 2, showed root:shoot ratio and LA attributes of maize genotypes under waterlogging conditions at different days of growth. Generally, water logging stress caused a substantial decline in crop growth potential viz., root growth and LA. However, root parameters in the present study exhibited differential responses, with increase in root length during the early seedling stage and a consequent rise in the root:shoot ratio (weight based) in the BML7 genotype. Also, the interaction analysis revealed that the maximum root:shoot ratio (0.23) was observed on 17th day in both the genotypes and similarly 27th day root:shoot ratio was also statistically at par for BML7 and BML6 under waterlogging condition.

Our investigation revealed a significant augmentation in the root:shoot ratio by fresh weight under waterlogging stress conditions compared to the control group. This increase in the root: shoot ratio was further exacerbated with escalating waterlogging stress durations. However, these findings diverge from previous reports, that found a decreasing trend in root:shoot ratio under waterlogging stress in maize (9, 13 & 19). This discrepancy likely underscores the substantial genotypic variability in plant responses to waterlogging stress. Furthermore, the absence of a significant genotypic interaction between BML6 and BML7 suggests that these genotypes exhibit relatively similar responses to waterlogging stress at a specific growth stage.

LA is a critical determinant of plant growth and yield, directly influencing photosynthetic capacity and ultimately dry matter production. In this study, waterlogging stress significantly reduced LA growth in both BML6 and BML7 genotypes. However, BML7 exhibited a more resilient response, showing a notable 20 % increase in LA on day 27 of waterlogging compared to the control. This difference was statistically significant ($p \leq 0.05$) between BML6 and BML7 (Table 3). The prolonged duration of waterlogging impeded plant growth, resulting in a reduction of both leaf number and leaf size. This reduction in LA likely resulted from a combination of factors, including reduced cell expansion, premature leaf senescence and the inhibition of leaf initiation. These findings are consistent with previous observations in other crops, including green gram and pigeonpea (24, 35 & 36). These findings underscore the importance of LA as a sensitive indicator of waterlogging stress in maize genotypes and highlight the potential for genotypic variation in the ability to maintain LA under such conditions. This information can be valuable for developing breeding strategies to improve waterlogging tolerance in maize.

Physiological changes in maize seedlings under different days of waterlogging

Waterlogging is a significant abiotic stress that profoundly affects plant growth and development. It leads to a cascade of physiological and biochemical alterations, including impaired gas exchange, nutrient deficiencies and oxidative stress. Among the key physiological parameters affected by waterlogging is chlorophyll content, a crucial determinant of photosynthetic efficiency and ultimately, crop yield (37).

This study investigated the impact of waterlogging stress on chlorophyll content in two maize genotypes (BML6 and BML7). Although no statistically significant differences in total chlorophyll content were observed between the stressed and

Table 1. Morphological alteration of maize seedlings: Plant height and root length under control and waterlogging conditions at seedling stages (Set 1 and Set 2)

Plant height (cm)										Root length (cm)									
Set 1	BML6		BML7		Set 2	BML6		BML7		Set 1	BML6		BML7		Set 2	BML6		BML 7	
Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL
11	37.0	37.6	37.9	38.6	21	60.6	61.0	59.6	56.6	11	9.98	9.38	9.60	9.88	21	16.2	15.8	17.0	17.0
13	42.3	40.8	42.3	41.0	23	66.6	63.0	70.8	61.2	13	11.4	13.8	11.6	15.5	23	16.7	20.8	19.1	18.5
15	46.0	42.9	48.0	45.1	25	72.4	67.2	74.0	69.0	15	11.7	15.2	13.2	17.8	25	18.7	23.6	20.1	25.9
17	51.7	48.0	51.1	51.5	27	80.2	76.9	79.6	76.2	17	13.2	19.8	16.4	20.7	27	21.7	28.2	20.6	29.6
Factors			C.D.	SE(±)			C.D.	SE(±)				C.D.	SE(±)					C.D.	SE (±)
Factor (V)			0.83	0.29			NS	0.40				0.34	0.12					0.54	0.19
Factor (C)			0.83	0.29			1.12	0.40				0.34	0.12					0.54	0.19
Interaction V X C			NS	0.42			1.59	0.56				NS	0.17					NS	0.27
Factor (S)			1.18	0.42			1.59	0.56				0.48	0.17					0.76	0.27
Interaction V X S			NS	0.59			2.25	0.79				0.67	0.24					NS	0.38
Interaction C X S			1.66	0.59			2.25	0.79				0.67	0.24					1.07	0.38
Interaction V X C X S			NS	0.83			NS	1.12				0.95	0.34					1.51	0.54

Ct= control; WL = waterlogging; BML6 and BML7 = maize genotypes; day = days after sowing; C.D. = critical difference at p ≤ 0.05; SE(±) = standard error; V = genotype; C = condition; S = stage; NS = non significant.

Table 2. Morphological alteration of maize seedlings: Root:shoot ratio and LA under control and waterlogging conditions at seedling stages (Set 1 and Set 2)

Root:Shoot										LA (cm^2)									
Set 1	BML6		BML7		Set 2	BML6		BML7		Set 1	BML6		BML7		Set 2	BML6		BML 7	
Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL
11	0.06	0.06	0.05	0.06	21	0.10	0.12	0.09	0.06	11	24.22	25.39	25.12	25.57	21	59.05	50.04	61.83	59.30
13	0.11	0.10	0.11	0.10	23	0.09	0.13	0.09	0.17	13	30.95	28.21	31.75	30.67	23	65.41	74.10	70.93	68.31
15	0.11	0.19	0.09	0.20	25	0.09	0.19	0.08	0.20	15	37.93	37.33	38.67	34.75	25	91.22	85.14	89.29	84.11
17	0.09	0.23	0.12	0.23	27	0.06	0.25	0.10	0.24	17	48.85	47.06	54.08	45.92	27	104.4	92.09	120.2	113.6
Factors			C.D.	SE(±)			C.D.	SE(±)				C.D.	SE(±)					C.D.	SE(±)
Factor (V)			NS	0.00			NS	0.00				1.05	0.37					2.45	0.87
Factor (C)			0.00	0.00			0.00	0.00				1.49	0.37					2.45	0.87
Interaction V X C			NS	0.00			0.00	0.00				1.49	0.53					NS	1.23
Factor (S)			0.00	0.00			0.00	0.00				NS	0.53					3.46	1.23
Interaction V X S			0.01	0.00			0.01	0.00				2.11	0.75					4.89	1.73
Interaction C X S			0.01	0.00			0.01	0.00				NS	0.75					4.89	1.73
Interaction V X C X S			0.01	0.00			0.01	0.00				1.05	0.37					2.45	0.87

Ct = control; WL = waterlogging; BML6 and BML7 = maize genotypes; day = days after sowing; C.D. = critical difference at p ≤ 0.05; SE(±) = standard error; V = genotype; C = condition; S = stage; NS = not significant.

Table 3. Analysis of variance (ANOVA) for the morphological traits evaluated under control and waterlogging condition (Set 1 and Set 2)

Sources of variation	df	Plant height	Root length	Root:Shoot	LA
Set 1 Mean sum of square					
Factor (V)	1	26.45**	35.32**	0.00 NS	13.61 NS
Factor (C)	1	36.45**	201.46**	0.06**	86.83**
Interaction V X C	1	6.61 NS	0.09 NS	0.00 NS	23.85*
Factor (S)	3	599.44**	208.76**	0.05**	2,13**
Interaction V X S	3	3.56 NS	5.21**	0.00**	8.77 NS
Interaction C X S	3	11.36*	29.11**	0.02**	27.98**
Interaction V X C X S	3	4.84 NS	3.52**	0.01**	14.87*
Error	64	3.46	0.57	0	5.57
Set 2 Mean sum of square					
Sources of variation	**df**	**Plant height**	**Root length**	**Root:Shoot**	**LA**
Factor (V)	1	0.253 NS	11.750**	0.00 NS	660.231**
Factor (C)	1	334.153**	268.659**	0.14**	401.692**
Interaction V X C	1	27.028*	0.228 NS	0.01**	0.472 NS
Factor (S)	3	1271.278**	279.046**	0.02**	9436.846**
Interaction V X S	3	19.986*	3.508 NS	0.03**	419.703**
Interaction C X S	3	26.086**	63.478**	0.03**	142.217**
Interaction V X C X S	3	10.828 NS	12.065**	0.03**	81.240*
Error	64	6.311	1.435	0	29.990

V = genotype (BML6 & BML7); C = condition (control and waterlogging); S = stage (days after sowing); LA=Leaf Area; df = degrees of freedom; NS = non significant; ** = significant at $p \leq 0.01$; * = significant at $p \leq 0.05$.

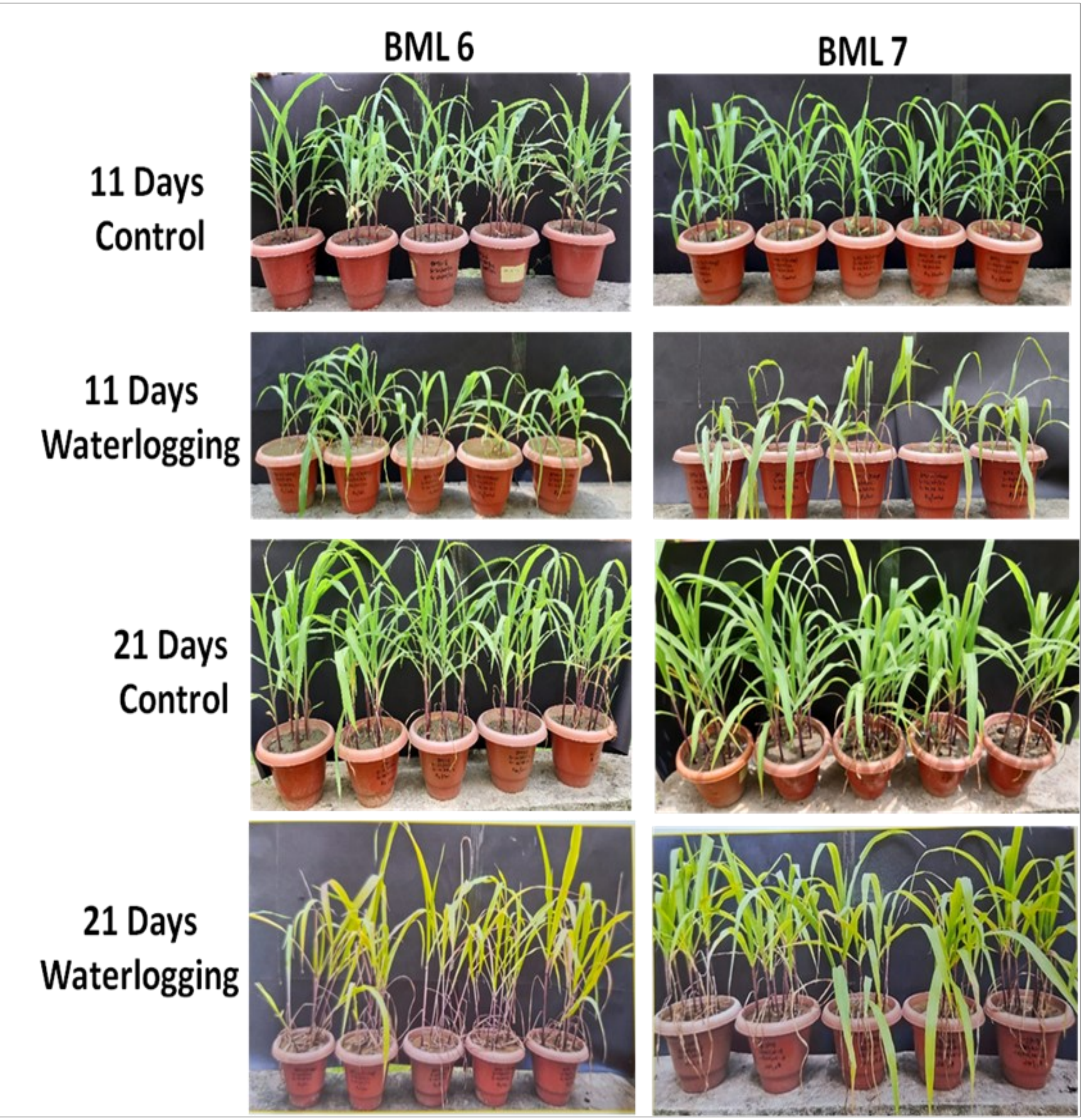

Fig. 1. Leaf senescence under control and waterlogged conditions in BML6 and BML7 at seedling stage Set 1 (11 days) and Set 2 (21 days).

control conditions in either genotype, a genotypic variation was evident. BML7 consistently exhibited higher chlorophyll levels compared to BML6 under both control and waterlogging conditions, suggesting a relatively better physiological performance and potential for sustained photosynthetic activity in the tolerant genotype. For example, under waterlogging conditions on the 17th day, BML7 exhibited a total chlorophyll content of 5.904 mg g^{-1} fr wt, while BML6 showed a lower content of 4.86 mg g^{-1} fr wt (Table 4).

However, waterlogging stress significantly reduced total chlorophyll content in both genotypes compared to their respective controls. In the control condition on the 17th day, BML7 had a total chlorophyll content of 7.740 mg g^{-1} fr wt, demonstrating the significant reduction caused by waterlogging. The observed decline may be due to multiple physiological disruptions. Waterlogging stress can induce the activity of chlorophyllase, an enzyme that catalyzes the degradation of chlorophyll. Previous studies have reported increased chlorophyllase activity in maize under waterlogged conditions (14, 23 & 38). Furthermore, waterlogging stress can disrupt the biosynthesis pathway of chlorophyll, leading to reduced chlorophyll production. This can be attributed to factors such as nutrient deficiencies (e.g., iron, magnesium), impaired carbon assimilation and oxidative damage to photosynthetic machinery.

ANOVA revealed significant interactions between genotype, stage and waterlogging on total chlorophyll content (Table 5). Control plants consistently exhibited higher chlorophyll levels than waterlogged plants across all stages and genotypes studied. Significant effects of genotype, waterlogging and stage were observed on total chlorophyll content. BML7 consistently displayed higher chlorophyll levels than BML6 and both genotypes responded more favourably to control conditions. These findings are consistent with previous research demonstrating the detrimental effects of waterlogging on chlorophyll content in various cereals crops, including rice and wheat (39). Waterlogging stress in these crops has been shown to induce chlorophyll degradation, inhibit chlorophyll synthesis and ultimately impair photosynthetic capacity. CSI was relatively less affected by waterlogging stress in this study. While a slight decrease in CSI was observed with prolonged waterlogging, these changes were non-significant across all treatments for both sets (Set 1 and Set 2) in both BML6 and BML7 genotypes. Consequently, ANOVA analysis did not reveal any significant effects of genotype, waterlogging or stage on CSI. Under stress conditions, plants with higher CSI values typically exhibit better tolerance to chlorophyll degradation. A higher CSI indicates the ability of the plant to maintain chlorophyll content despite stress-induced degradation. In this study, both BML6 and BML7 maintained CSI values within a narrow range (74 - 82 %) throughout

Table 4. Physiological alteration of maize seedlings grown under control and waterlogging conditions at stages of seedlings Set 1 and Set 2

	RWC (%)				Total Chlorophyll Content (mg g^{-1} fr wt)				CSI (%)			
Set 1	**BML6**		**BML7**		**BML6**		**BML7**		**BML6**		**BML7**	
	Ct	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**
11 day	81.50	81.00	81.00	80.50	4.88	4.76	5.46	5.34	81.80	82.00	81.80	82.00
13 day	82.47	78.66	81.95	79.35	6.17	5.46	6.78	6.69	82.10	81.22	82.10	81.22
15 day	83.55	72.22	82.75	74.56	6.66	5.19	7.04	6.28	82.26	80.62	82.26	80.62
17 day	85.50	67.50	83.25	69.25	6.99	4.86	7.74	5.94	81.83	79.56	81.83	79.56
SE(±)	1..60	1.91	2.07	2.01	0.14	0.12	2.17	2.1	2.25	2.10	2.25	2.10
CD	NS	5.9	NS	6.2	0.35	0.4	8.34	7.61	NS	NS	NS	NS
Set 2	**BML6**		**BML7**		**BML6**		**BML7**		**BML6**		**BML7**	
	Ct	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**	**Ct**	**WL**
21 day	81.00	82.00	82.20	81.15	4.74	4.88	5.48	5.34	82.10	82.04	82.10	82.04
23 day	82.55	77.20	82.77	79.50	6.17	5.46	6.72	6.70	81.57	80.14	81.57	80.14
25 day	83.67	71.32	83.90	74.00	6.66	5.20	7.04	6.28	80.95	77.96	80.95	77.96
27 day	84.25	65.00	84.50	69.54	6.99	4.85	7.78	5.94	79.39	74.74	79.39	74.74
SE(±)	2.17	1.93	2.16	1.98	0.14	0.35	2.18	2.00	2.38	2.08	2.38	2.08
CD	NS	5.9	NS	6.1	0.42	1.23	8.22	6.49	NS	NS	NS	NS

Ct = control; WL = waterlogging; BML6 and BML7 = maize genotypes; se(±) = standard error; CD = critical difference at $p \leq 0.05$; NS = non significant; fr wt = fresh weight.

Table 5. Analysis of variance (ANOVA) for the physio-biochemical traits evaluated under control and waterlogging condition

		Mean sum of square (Set 1)					
Sources of variation	**Df**	**Total Chl**	**CSI**	**RWC**	**Total Carbohydrate**	**H_2O_2**	**POD**
Factor (V)	1	11.842**	10.636^{NS}	0.024**	80.565^{NS}	0.121^{NS}	177.461**
Factor (C)	1	14.637**	78.745^{NS}	1085.232**	4941.783**	16,651.395**	2556.012**
Interaction V X C	1	0.689**	14.073^{NS}	21.767^{NS}	228.277**	0.118^{NS}	35.640^{NS}
Factor (S)	3	7.490**	0.189^{NS}	93.280**	5,350.364**	3240.179**	765.707**
Interaction V X S	3	0.123^{NS}	4.259^{NS}	1.532^{NS}	56.203^{NS}	11.657^{NS}	5.233^{NS}
Interaction C X S	3	3.970**	19.194^{NS}	241.197**	450.653**	2,964.324**	340.212**
Interaction V X C X S	3	0.232*	4.182^{NS}	4.123^{NS}	39.303^{NS}	12.043*	7.636^{NS}
Error	64	0.081	23.968	20.174	21.689	4.485	9.784
		Mean sum of square (Set 2)					
Factor (V)	1	11.874**	31.630^{NS}	34.98^{NS}	76.11^{NS}	17.574^{NS}	364.636**
Factor (C)	1	14.655**	347.918**	1325.63**	926.49**	19088.22**	2082.942**
InteractionV X C	1	0.695**	71.093^{NS}	14.22^{NS}	84.05*	28.65*	17.117^{NS}
Factor (S)	3	7.467**	44.461^{NS}	131.07**	2048.22**	4240.99**	1691.985**
Interaction V X S	3	0.123^{NS}	8.802^{NS}	4.12^{NS}	28.25^{NS}	14.25*	175.118**
Interaction C X S	3	3.964**	62.860^{NS}	282.96**	70.09*	3778.61**	463.282**
Interaction V X C X S	3	0.229**	12.247^{NS}	8.98^{NS}	5.950^{NS}	22.55**	99.191**
Error	64	0.054	25.191	22.19	20.97	5.293	9.899

V = genotypes (BML6 & BML7); C = condition (control and waterlogging); S = stage (days after sowing); Df = degrees of freedom; NS = non significant; ** = significant at $p \leq 0.01$; * = significant at $p \leq 0.05$.

the experiment, regardless of growth stage or waterlogging duration. These findings suggest that both genotypes possess a certain degree of resilience to waterlogging stress, enabling them to maintain relatively stable chlorophyll levels even under prolonged waterlogging conditions.

The relatively stable CSI values in both genotypes may be attributed to several factors. Genotypes may possess efficient mechanisms for chlorophyll protection, such as enhanced synthesis of antioxidant compounds like SOD, CAT and ascorbate peroxidase (APX), which scavenge ROS generated during waterlogging stress. Additionally, pathways involving the ascorbate-glutathione cycle and upregulation of non-enzymatic antioxidants such as ascorbic acid and glutathione contribute to mitigating oxidative damage and preserving chlorophyll integrity. ROS can cause oxidative damage to chlorophyll molecules, leading to degradation. Secondly, the genotypes may have effective mechanisms for repairing or replacing damaged chlorophyll molecules. This could involve the upregulation of genes involved in chlorophyll biosynthesis or the activation of repair pathways. Further research is needed to elucidate the specific mechanisms underlying the relatively stable CSI values observed in these maize genotypes. Investigating the activities of antioxidant enzymes, the expression of genes involved in chlorophyll biosynthesis and degradation and the levels of ROS in these genotypes under waterlogging stress could provide valuable insights into their resilience to chlorophyll degradation (23, 32 & 40).

RWC serves as a crucial indicator of plant water status, reflecting the plant's ability to maintain adequate hydration under stress conditions. A decline in RWC signifies cellular dehydration, which can significantly impact various physiological processes including photosynthesis, respiration and ultimately the crop yield (37, 39 & 40).

In this study, we observed a consistent decline in RWC in both maize genotypes (BML6 and BML7) under increasing durations of waterlogging stress compared to the control conditions at both the 11th and 21st day stages. This decrease in RWC is a direct consequence of the restricted oxygen availability and impeded water uptake from the waterlogged soil, leading to cellular dehydration. The severity of RWC reduction varied between genotypes. Genotype BML7 consistently exhibited higher RWC values than BML6 under waterlogging stress, suggesting a greater capacity to maintain cellular hydration. The lowest RWC observed was 65 % in genotype BML6 on the 27th day of waterlogging. In contrast, BML7 maintained a higher RWC, with a minimum of 75.82 % on the 27th day followed by a slight recovery on the 25th day.

These findings align with previous studies demonstrating the negative impact of waterlogging on RWC in various crops. For instance, in green gram, pigeon pea and rice, reduced RWC under waterlogging stress has been shown to significantly impair growth, development and yield (35, 36 & 40). Decreased RWC leads to a reduction in cell turgor pressure, which can affect cell expansion, stomatal closure and overall plant growth. Dehydrated cells experience reduced photosynthetic activity due to factors such as stomatal closure, decreased enzyme activity and damage to the photosynthetic apparatus. Cellular dehydration can also disrupt various metabolic processes, including protein synthesis, respiration and nutrient uptake. The observed decline in RWC in both maize genotypes under waterlogging stress highlights the significant impact of this abiotic stress on plant water status. Genotype BML7 demonstrated a greater capacity to maintain higher RWC compared to BML6, suggesting a potential advantage in terms of water stress tolerance. These findings emphasize the importance of RWC as a crucial indicator of plant water status and its critical role in determining plant performance under waterlogging stress. Further research is warranted to investigate the underlying mechanisms of RWC maintenance in the more tolerant genotype (BML7). This could involve examining factors such as root system architecture, aquaporin activity and the accumulation of osmoprotectants (9, 32). Understanding these mechanisms could provide valuable insights for developing waterlogging-tolerant maize cultivars (35).

Biochemical changes in maize seedlings under different days of waterlogging

Biochemical alteration in maize genotypes was studied under different days of waterlogging conditions. During waterlogging, the generation of ROS, particularly H_2O_2, along with the activation of antioxidative enzymes such as peroxidase (POD), is common and immediate responses of plants to oxidative stress (40-42). To cope with ROS and maintain redox-homeostasis, plants have developed a well-integrated antioxidant defence system, which is composed of antioxidant molecules and antioxidant enzymes, such as SOD, CAT and enzymes involved in the ascorbate - glutathione cycle (43). Therefore, these parameters were assessed in the study and results showed three folds increase in generation of H_2O_2 (92.28 μ mol g^{-1} fr wt) under waterlogging stress from control (31.82 μ mol g^{-1} fr wt) on 25th DAG in genotype BML7 and was noted to be statistically superior to control condition (Table 6).

The analysis of variance for H_2O_2 for 11 day and 21 day seedling revealed that the main effect of condition was found to be highly significant where as the main effect of genotypes and the interaction effect of Condition (C) and stages (S) with genotypes were found to be non-significant. So far as the interaction of C with S showed that in the control condition, the highest generation of H_2O_2 was observed on 25th and 27th DAG. However, waterlogged condition showed increasing trend up to 25th day where after H_2O_2 was significantly declined at 27th DAG in both sets of both the genotypes BML6 and BML7.

POD activity progressively increased with waterlogging condition having mode of scavenging the ROS generated during the stress with more of POD activity in BML7 with 88.98 µmol H_2O_2 reduced mg^{-1} protein min^{-1} on 27th day of stress. This indicates the potential of this genotype in the detoxification of H_2O_2 efficiently in response to stress than that of BML6 and when compared with control condition.

The ANOVA for POD was found to be highly significant for both the sets, Set 1 and Set 2 whereby a perusal of two-way mean table of variety (V), condition (C) and stage (S) showed that the main effect of genotype BML7 was significantly superior to BML6. Furthermore, it was observed that C × S interaction indicated a consistent and significant increasing trend across stages under both control and waterlogging conditions, highlighting that POD activity progressively increased with stress as well as developmental stage. These increased levels of POD showed tolerance towards stress as reported in other crops also under different abiotic stresses (30, 44, 45). Therefore, the result

Table 6. Biochemical alterations in maize seedlings: levels of H_2O_2 and POD activity under control and waterlogging conditions at two seedling stages

H_2O_2 (μ molg^{-1} fr wt)										POD (μ mol H_2O_2 reduced mg^{-1} protein min^{-1})									
Set 1	BML6		BML7		Set2	BML6		BML7		Set 1	BML6		BML7		Set 2	BML6		BML 7	
Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL	Day	Ct	WL	Ct	WL
11	28.6	27.7	27.6	27.8	21	28.1	28.8	28.9	28.9	11	52.9	55.2	54.6	56.8	21	49.8	52.2	58.8	61.7
13	28.7	72.7	28.8	73.4	23	30.6	77.7	29.7	75.5	13	53.1	62.20	59.4	63.4	23	54.7	63.6	62.4	65.9
15	29.9	81.9	30.5	84.9	25	31.0	91.6	31.8	92.9	15	53.2	71.31	59.3	72.6	25	76.1	76.1	64.8	79.8
17	30.7	51.2	30.9	46.7	27	31.4	51.6	32.9	44.3	17	57.6	78.6	60.8	80.4	27	57.8	82.8	65.2	88.9

Factors	C.D.	SE(±)	C.D.	SE(±)	C.D.	SE(±)	C.D.	SE(±)
Factor (V)	NS	0.34	NS	0.36	1.40	0.50	1.41	0.50
Factor (C)	0.95	0.34	1.03	0.36	1.40	0.50	1.41	0.50
Interaction V X C	NS	0.47	1.45	0.51	NS	0.70	NS	0.70
Factor (S)	1.34	0.47	1.45	0.51	1.98	0.70	1.99	0.70
Interaction V X S	NS	0.67	NS	0.73	NS	0.99	2.81	1.00
Interaction C X S	1.89	0.67	2.06	0.73	2.80	0.99	2.81	1.00
Interaction V X C X S	NS	0.95	2.91	1.03	NS	1.40	3.98	1.41

Ct = control; WL = waterlogging; BML6 and BML7 = maize genotypes; SE(±) = standard error; CD = critical difference at $p \leq 0.05$; V = genotype; C = condition; S = stage; NS = non significant.

clearly indicated the higher scavenging ability of POD for generated H_2O_2 under stress in genotype BML7 than BML6.

Total carbohydrate content was observed to be in increasing pattern in both the genotypes under waterlogging from that of control however, the V × C × S interaction revealed no significant differences between the genotypes across stages (Table 7). In Set 1 maximum carbohydrate content was observed on 17th day with 144.53 mg g^{-1} fr wt and in Set 2 on 27th day with 192.55 mg g^{-1} fr wt in genotype BML6. Comparatively genotype BML6 showed higher carbohydrate content than genotype BML7. The genotype, condition and stages indicated that the main effect of genotype BML6 was significantly superior to BML7. In case of conditions, waterlogged condition was significantly superior to control condition and regarding the main effect of stages the maximum total carbohydrate was observed on 17th day followed by 15th day while the minimum was on 11th day followed by 13th day.

The interaction showed that in the control condition there was a significant increase trend from 11th to 17th day but in case of BML6 there was a significant increase up to 15th day and then it was at par with 17th. The maximum total carbohydrate was observed on 17th day (144.53 mg g^{-1} fr wt) as compared to control and 11th day (93.27 mg g^{-1} fr wt and 117.05 mg g^{-1} fr wt). Similarly in genotype BML7 waterlogged condition was statistically superior to control condition as regards main effects of stages. It was observed that the maximum total carbohydrate was observed on27th day (184.75 mg g-1 fr wt) followed by 25th day (171.52 mg g^{-1} fr wt) and the minimum value was 160.55 mg g^{-1} fr wt on 21st day followed by 23rd day (164.53 mg g^{-1} fr wt) respectively under waterlogged conditions.

Waterlogging resulted in a general increase in total carbohydrate accumulation in both maize genotypes across the stress period, with BML6 showing a slightly greater increase compared to BML7 at several time points. This pattern suggests a possible shift in carbon allocation or altered carbohydrate metabolism under stress conditions rather than depletion. Although reductions in total sugars under waterlogging are generally attributed to oxygen deficiency and hypoxic conditions, these stresses also reduce root activity, thereby limiting water uptake and inhibiting both the synthesis and translocation of photosynthetic assimilates (9, 43). The present results indicate a genotype-specific adaptive response. Previous studies have reported similar reductions in sugar content due to waterlogging in pigeonpea (24, 36) and maize (15, 17 & 46). The ANOVA results demonstrate that total carbohydrate content is significantly influenced by the main effects of treatment C, S and V, along with their interactions, particularly C × S and V × C, highlighting the complexity of the plant's response depending on genotype and developmental timing. These findings support earlier report that waterlogging disrupts carbon metabolism and antioxidant responses in summer maize, particularly when stress occurs at early developmental stages (47). However, maintaining of higher sugar content sustaining photosynthetic and metabolic stability has been reported in tolerant genotypes of barley under waterlogging

Table 7. Biochemical alterations in maize seedlings: total carbohydrate content under control and waterlogging conditions at two seedling stages

Total carbohydrate (mg g^{-1} fr wt)									
Set 1	BML6		BML7		Set 2	BML6		BML7	
	Ct	WL	Ct	WL		Ct	WL	Ct	WL
11 day	91.44	93.27	92.41	95.15	21 day	157.43	160.68	158.58	160.55
13 day	106.59	129.13	105.99	116.64	23 day	161.03	169.91	161.70	164.53
15 day	113.03	137.59	115.82	130.69	25 day	165.31	174.20	166.23	171.52
17 day	117.05	144.53	119.43	140.52	27 day	178.15	192.55	175.83	184.75
Factors			C.D.	SE(±)				C.D.	SE(±)
Factor (V)			NS	NS				NS	0.72
Factor (C)			2.08	2.08				2.05	0.72
Interaction V X C			2.94	2.94				2.89	1.02
Factor (S)			2.94	2.94				2.89	1.02
Interaction V X S			NS	NS				NS	1.45
Interaction C X S			4.16	4.16				4.09	1.45
Interaction V X C X S			NS	NS				NS	2.05

Ct = control; WL = waterlogging; BML6 and BML7 = maize genotypes; day = days after sowing; C.D. = critical difference at $p \leq 0.05$; SE(±) = standard error; V = genotype; C = condition; S = stage; NS = non significant.

conditions (48). The present study showed the different pattern with comparatively higher carbohydrate levels in susceptible genotype BML6, despite stress than tolerant genotype BML7, indicating more stable photosynthetic efficiency and carbon allocation, underscoring the importance of genotype-specific traits in conferring waterlogging tolerance.

The present study observed a reduced root:shoot ratio under prolonged waterlogging, particularly in the sensitive genotype BML6. Previous studies have also reported that both drought and waterlogging stress can alter the root:shoot balance and disrupt the source-sink relationship during grain filling, leading to impaired biomass partitioning and ultimately reducing yield potential (49). Although this study focused on the seedling stage, the trends in root development and photosynthate allocation observed may have downstream effects on reproductive development under field conditions. The overall findings further highlighted clear genotypic variations in stress responses across all the recorded parameters, thereby underscoring distinct differences between the two maize genotypes. These variations, summarized comprehensively in Fig. 2, provide an integrative overview of the entire study and reinforce the significance of genotype-specific adaptive strategies under waterlogging stress. Furthermore, these results highlight the importance of investigating genotype-specific adaptive responses at physiological and metabolic levels under variable water stress conditions.

Conclusion

In conclusion, waterlogging stress markedly impaired maize growth and physiology, with pronounced reductions in plant height, LA, chlorophyll content and RWC, particularly in the susceptible genotype BML6. Despite these setbacks, root length and root:shoot ratio increased under stress, especially in BML7, indicating adaptive root plasticity. BML7 also demonstrated superior tolerance through higher RWC, chlorophyll stability and enhanced antioxidative defence (e.g., elevated POD activity and moderated H_2O_2 accumulation), highlighting its better stress resilience. Biochemical responses varied, with BML6 accumulating

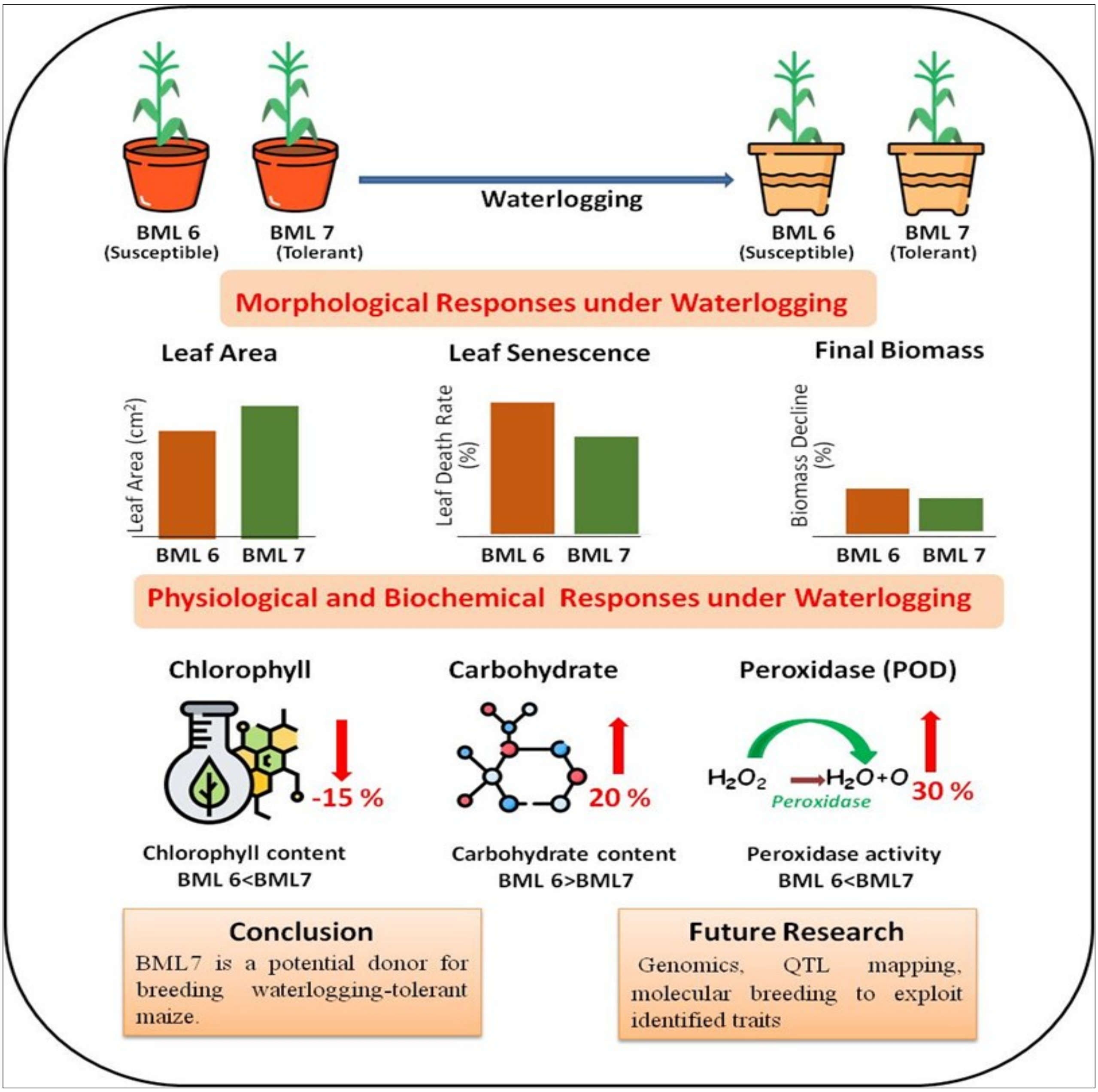

Fig. 2. Summary of the morpho-physiological and biochemical responses of two maize genotypes (BML6 – susceptible, BML7 - tolerant) under different days of waterlogging conditions.

more carbohydrates initially, but BML7 sustains better metabolic activity under prolonged stress. These findings underscore genotypic variability in waterlogging tolerance and suggest BML7 as a promising genetic resource for breeding programs targeting improved resilience to waterlogged conditions.

Acknowledgements

The authors acknowledge the Bihar Agricultural University, Sabour, Bihar for the laboratory facilities to carried out the experiments. The Fig. 2 of this manuscript was created using resources from Flaticon.com and the authors acknowledge the following icon artists: Eucalyp, Freepik and Smashicons. This manuscript has BAU Communication Number 1364/221201.

Authors' contributions

SN and MPM designed the study. MT conducted the experiments. SN and MT conceived the structure of the manuscript. RK and TR helped in data analyses. SSM contribute in manuscript preparation.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. Jackson MB, Colmer TD. Response and adaptation by plants to flooding stress. Ann Bot. 2005;96(4):501–5. https://doi.org/10.1093/aob/mci205
2. Aggarwal PK, Kalra N, Chander S, Pathak H. Info Crop: a dynamic simulation model for the assessment of crop yields, losses due to pests and environmental impact of agro-ecosystems in tropical environments. I. Model description. Agric Syst. 2006;89(1):1-25. https://doi.org/10.1016/j.agsy.2005.08.001
3. Voesenek LA, Colmer TD, Pierik R, Millenaar FF, Peeters AJ. How plants cope with complete submergence. New Phytol. 2006;170:213-26. https://doi.org/10.1111/j.1469-8137.2006.01692.x
4. Ferreira JL, Magalhaes PC, Borem A. Evaluation of three physiologic characteristics in four cycles of selection in maize cultivar BRS-4154 under tolerance to waterlogging of the soil. Cienc Agrotec. 2008;32:1719–23. https://doi.org/10.1590/S1413-70542008000600006
5. Dat JF, Capelli N, Folzer H, Bourgeade P, Badot PM. Sensing and signalling during plant flooding. Plant Physiol Biochem. 2004;42(4):273-82. https://doi.org/10.1016/j.plaphy.2004.02.003
6. Bailey-Serres J, Voesenek LACJ. Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol. 2008;59:313–39. https://doi.org/10.1146/annurev.arplant.59.032607.092752
7. FAOSTAT. Food and Agriculture Organization of the United Nations. Rome: FAO. 2023.
8. Intergovernmental Panel on Climate Change (IPCC). Climate Change 2021: The Physical Science Basis. Cambridge: Cambridge University Press. 2021.
9. Zaidi PH, Rafique S, Rai PK, Singh NN, Srinivasan G. Tolerance to excess moisture in maize (*Zea mays* L.): susceptible crop stages and identification of tolerant genotypes. Field Crops Res. 2004;90(2-3):189-202. https://doi.org/10.1016/j.fcr.2004.03.002
10. Kaur G, Vikal Y, Kaur L, Kalia A, Mittal A, Kaur D, et al. Elucidating the morpho-physiological adaptations and molecular responses under long-term waterlogging stress in maize through gene expression analysis. Plant Sci. 2021;304:110823. https://doi.org/10.1016/j.plantsci.2021.110823
11. Shi F, Yamamoto R, Shimamura S, Hiraga S, Nakayama N, Nakamura T, et al. Cytosolic ascorbate peroxidase 2 (cAPX2) is involved in the soybean response to flooding. Phytochemistry. 2008;69:1295-303. https://doi.org/10.1016/j.phytochem.2008.01.007
12. Hashiguchi A, Sakata K, Komatsu S. Proteome analysis of early-stage soybean seedlings under flooding stress. J Proteome Res. 2009;8(4):2058–69. https://doi.org/10.1021/pr801051m
13. Younis ME, El-Shahaby OA, Nemat AMM, El-Basatwisky MZ. Kinetin alleviates the influence of waterlogging and salinity on growth and affects the production of plant growth regulators in *Vigna sinensis* and *Zea mays*. Agronomy. 2003;23:277-85. https://doi.org/10.1051/agro:2003010
14. Baranwal S, Singh BB. Effect of waterlogging on growth, chlorophylls and saccharides content in maize genotypes. Indian J Plant Physiol. 2002;7:246–51. https://doi.org/10.5897/AJAR2015.9790
15. Lone AA, Warsi MZK. Response of maize (*Zea mays* L.) to excess soil moisture tolerance at different stages of life cycle. Bot Res Int. 2009;2(3):211-7.
16. Alam I, Sharmin SA, Kim KH, Yang JK, Choi MS, Lee BH. Proteome analysis of soybean roots subjected to short-term drought stress. Plant Soil. 2010;333(1):491–505. https://doi.org/10.1007/s11104-010-0365-7
17. Ren B, Zhang J, Li X, Fan X, Dong S, Liu P, et al. Effects of waterlogging on the yield and growth of summer maize under field conditions. Can J Plant Sci. 2014;94(1):23–31. https://doi.org/10.4141/cjps2013-175
18. Tian LX, Bi WS, Ren XS, Li WL, Sun L, Li J. Flooding has more adverse effects on the stem structure and yield of spring maize (*Zea mays* L.) than waterlogging in Northeast China. Eur J Agron. 2020;117:126054. https://doi.org/10.1016/j.eja.2020.126054
19. Zaidi PH, Rafique S, Singh NN. Response of maize (*Zea mays* L.) genotypes to excess soil moisture stress: morpho-physiological effects and basis of tolerance. Eur J Agron. 2003;19(3):383-99. https://doi.org/10.1016/S1161-0301(02)00090-4
20. Yordanova RY, Popova LP. Flooding-induced changes in photosynthesis and oxidative status in maize plants. Acta Physiol Plant. 2007;29:535-41. https://doi.org/10.1007/s11738-007-0064-z
21. Shin S, Kim SG, Jung GH, Kim CG, Son BY, Kim JT, et al. Evaluation of waterlogging tolerance with the degree of foliar senescence at early vegetative stage of maize (*Zea mays* L.). J Crop Sci Biotechnol. 2016;19:393–9. https://doi.org/10.1007/s12892-016-0097-1
22. Pociecha E, Koscielniak J, Filek W. Effects of root flooding and stage of development on the growth and photosynthesis of field bean (*Vicia faba* L. minor). Acta Physiol Plant. 2008;30:529–35. https://doi.org/10.1007/s11738-008-0151-9
23. Else MA, Janowiak F, Atkinson CJ, Jackson MB. Root signals and stomatal closure in relation to photosynthesis, chlorophyll a fluorescence and adventitious rooting of flooded tomato plants. Ann Bot. 2009;103:313–23. https://doi.org/10.1093/aob/mcn208
24. Celik G, Turhan E. Genotypic variation in growth and physiological responses of common bean (*Phaseolus vulgaris* L.) seedlings to flooding. Afr J Biotechnol. 2011;10(38):7372–80. https://doi.org/10.5897/AJB11.500
25. Jahan MS, Nordin MNB, Lah MKBC, Khanif YM. Effects of water stress on rice production: bioavailability of potassium in soil. J Stress Physiol Biochem. 2013;9(2):97–107.
26. Rai RK, Srivastava JP, Shahi JP. Effect of waterlogging on some biochemical parameters during early growth stages of maize. Indian J Plant Physiol. 2004;9:65–8.
27. Guo W, Xing Y, Luo X, Li F, Ren M, Liang Y. Reactive oxygen species: a

crosslink between plant and human eukaryotic cell systems. Int J Mol Sci. 2023;24(17):13052. https://doi.org/10.3390/ijms241713052

28. Blokhina OB, Chirkova TV, Fagerstedt KV. Anoxic stress leads to hydrogen peroxide formation in plant cells. J Exp Bot. 2001;52 (359):1179–90. https://doi.org/10.1093/jexbot/52.359.1179

29. Corpas FJ, Fernandez-Ocana A, Carreras A, Valderrama R, Luque F, Esteban FJ, et al. The expression of different superoxide dismutase forms is cell-type dependent in olive (*Olea europaea* L.) leaves. Plant Cell Physiol. 2006;47(7):984–94. https://doi.org/10.1093/pcp/pcj071

30. Lama R, Jaishee N, Chakraborty U, Roy A. Responses of seven maize genotypes during flooding stress and identification of cultivars most tolerant to flooding conditions. Plant Arch. 2020;20(2):3244–9.

31. Arnon DI. Copper enzymes in isolated chloroplasts, polyphenoxidase in *Beta vulgaris*. Plant Physiol. 1949;24:1-15. https://doi.org/10.1104/pp.24.1.1

32. Nahakpam S, Shah K. Expression of key antioxidant enzymes under combined effect of heat and cadmium toxicity in growing rice seedlings. Plant Growth Regul. 2011;63:23-35. https://doi.org/10.1007/s10725-010-9508-3

33. Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F. Colorimetric method for determination of sugars and related substances. Anal Chem. 1956;28:350-6. https://doi.org/10.1021/ac60111a017

34. Ali S, Kim WC. Plant growth promotion under water: decrease of waterlogging-induced ACC and ethylene levels by ACC deaminase-producing bacteria. Front Microbiol. 2018;9:1096. https://doi.org/10.3389/fmicb.2018.01096

35. Joshi R, Bhattacharya P, Lekshmy S, Sairam RK. Physiological traits to screen mungbean genotypes for waterlogging tolerance in a subtropical environment. In: National Conference of Plant Physiology on Physiological and Molecular Approaches for Crop Improvement under Changing Environment; 2010 Nov 25-27; Varanasi, India. p.125.

36. Kumutha D, Ezhilmathi K, Sairam RK, Srivastava GC, Deshmukh PS, Meena RC. Waterlogging induced oxidative stress and antioxidant activity in pigeonpea genotypes. Biol Plant. 2009;53(1):75-84. https://doi.org/10.1007/s10535-009-0011-5

37. Nahakpam S. Effectual tolerant traits for grain yield in rice genotypes grown under drought. J Pharmacogn Phytochem. 2017a;1:890-7.

38. Kumari A, Pandey OP. Effect of waterlogging on metabolic constituents in maize. Indian J Plant Physiol. 2007;12(4):366. https://doi.org/10.3390/plants13010108

39. Nahakpam S. Chlorophyll stability: a better trait for grain yield in rice under drought. Indian J Ecol. 2017b;44(4):77-82.

40. Nahakpam S, Kesari R, Singh SP, Pal AK, Satyendra, Sinha S, et al. Essential traits for reproductive drought and heat stress tolerance of Sabour Ardhjal rice: implication for agricultural improvement. Int J Adv Biochem Res. 2024;8(9):598–606. https://doi.org/10.33545/26174693.2024.v8.i9h.2244

41. Waraich EA, Ahmad R, Ashraf MY. Improving agricultural water use efficiency by nutrient management in crop plants. Acta Agric Scand B Soil Plant Sci. 2011;61(4):291–304. https://doi.org/10.1080/09064710.2010.491954

42. Bharti A, Kesari R, Sinha S, Nahakpam S, Kumar M, Roy C. Mechanistic insights and genetic approaches for enhancing submergence tolerance in rice. J Exp Agric Int. 2024;47(8):1037–51. https://doi.org/10.9734/jeai/2024/v46i82792

43. Shah K, Nahakpam S. Heat stress and cadmium toxicity in higher plants: an overview. In: Hemantaranjan A, editor. Adv Plant Physiol. Vol. 12. Jodhpur (India): Scientific Publishers; 2011. p.243-80.

44. Bin T, Xu SZ, Zou XL, Zheng YL, Qiu FZ. Changes of antioxidative enzymes and lipid peroxidation in leaves and roots of waterlogging-tolerant and waterlogging-sensitive maize genotypes at seedling stage. Agric Sci China. 2010;9(5):651–61. https://doi.org/10.1016/S1671-2927(09)60140-1

45. Akter T, Saquib TMN, Islam MR, Ali MR, Motiar M, Rohman M. Comparative analysis of physiological and anti-oxidative enzyme responses of maize genotypes under waterlogging stress and screening of tolerant genotypes. Plant Omics J. 2021;14(1):64–71. https://doi.org/10.21475/POJ.14.01.21.p3211

46. Kulkarni SS, Chavan PD. Influence of waterlogging on carbohydrate metabolism in ragi and rice roots. J Stress Physiol Biochem. 2013;9 (2):199-205.

47. Ren B, Zhang J, Dong S, Liu P, Zhao B. Responses of carbon metabolism and antioxidant system of summer maize to waterlogging at different stages. J Agron Crop Sci. 2018;204(5):505-14. https://doi.org/10.1111/jac.12275

48. Wang F, Zhou Z, Liu X, Zhu L, Guo B, Lv C, et al. Transcriptome and metabolome analyses reveal molecular insights into waterlogging tolerance in barley. BMC Plant Biol. 2024;24:385. https://doi.org/10.1186/s12870-024-05091-8

49. Zhao HR, Zhang L, Qi Y, Yang C, Hu LL. Effects of drought and waterlogging stress on root-shoot ratio and source-sink relationship of grain filling of summer maize. Clim Change Res. 2024;20(6):782-98. https://doi.org/10.12006/j.issn.1673-1719

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.