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RESEARCH ARTICLE

Physiological effects of stress-related enzymes and reactive oxygen species in chilli (*Capsicum annum* L.) genotypes under waterlogging conditions

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Abstract

The experiment involved two sets and was conducted to investigate the responses of various chilli genotypes to waterlogging in the net house of the Department of Plant Physiology, College of Agriculture, OUAT, Bhubaneswar. Initially, eight chilli varieties underwent trials exposed to different durations of waterlogging. Notably, local varieties Barkote and Daringbadi exhibited exceptional resilience regarding adventitious root formation, yellowing of leaves and wilting %. These were further studied in the second experiment where the plants of local genotypes, when subjected to waterlogging for specific durations of 2 h, 4 h, 6 h and 8 h, displayed decreased growth with sudden wilting syndrome, a physiological disorder. This short exposure to waterlogging led to an oxidative burst, resulting in elevated levels of Reactive Oxygen Species (ROS) like H_2O_2 and O_2^- and intensified membrane peroxidation and production of malondialdehyde (MDA) and superoxide dismutase (SOD) played a vital role in ROS defence, leading to higher antioxidant enzyme levels in Daringbadi, including catalase, peroxidase, SOD and glutathione peroxidase 66 %, 50.4 %, 35.7 % and 51.5 % higher, respectively. Glutathione reductase and ascorbic acid oxidase activities were 49.4 % and 39.2 % higher in barkote, revealing differing waterlogging resistance mechanisms in both varieties. Furthermore, the experiment showed that Barkote and Daringbadi experienced reduced yield components compared to their non-stressed counterparts. Daringbadi exhibited a more significant reduction in yield of 19.8 % than Barkote. Our study found that local chilli pepper cultivars (Daringbadi and Barkote) had a relatively tolerant ability to short-term waterlog for less than 12 h than all the tested varieties and Barkote excels to Daringbari. The study suggests that chilli breeding should considered between released and local species to expand genetic sources.

Keywords: *Capsicum annum*; ROS; MDA; stress enzymes; waterlogging

Introduction

Chilli, a fruit of the *'Capsicum annum'* plants from the solanaceae family, is a significant commercial crop in India, which leads the world in chilli production and exports, holding a 56.4 % share of the global market. Spanning 7.75 lakh hectares, India yields 14.92 lakh tonnes of chilli with a productivity rate of 1.9 tonnes per hectare. In Odisha, local farmers typically grow chilli during the dry season. However, in the past decade, unpredictable rainfall patterns have increasingly threatened chilli production due to waterlogged rhizosphere (WSR) conditions, which chilli plants are susceptible to. This sensitivity is mainly due to their shallow root systems, which suffer more than their above-ground parts. Among these parts, leaves are the most sensitive but can recover up to 81.5 % within seven days. Water stress significantly impacts yield (1). Chilli genotypes and landraces with robust root and shoot development exhibit greater tolerance to short-term waterlogging by sustaining turgor and osmotic adjustment in tolerant genotypes during the seedling stage. Under water stress conditions, a decrease in chlorophyll content indicates oxidative stress and can be attributed to chlorophyll photo-oxidation and degradation (2). In Odisha, chilli peaks during the drier post-monsoon and winter months (November- February) due to reduced rainfall, while lower yields are typical during the rainy monsoon season (June-September). Oxygen deprivation to vegetable roots can cause root failure and plant collapse, with limited recovery potential. Waterlogging stress generates excess reactive oxygen species (ROS), producing oxidative stress. ROS, including superoxide radical (O_2^-), hydroxyl radical (OH^-) and hydrogen peroxide (H_2O_2), are continuously produced as by-products of metabolic reactions. Against ROS, plants evolved antioxidant defence mechanisms (3) like superoxide dismutase (SOD), catalase (CAT) and Peroxidase (APX), regardless of growing conditions (field or pot) along with high malondialdehyde (MDA) (4). Nevertheless, the scarcity of research on chillis' reaction to waterlogging stress has led to a pot experiment to examine the impact of brief waterlogging exposure. This study aims to address the gaps in understanding of how chilli plants respond to waterlogging stress due to outbursts of ROS and scavenging enzymes challenging environmental conditions.

Materials and Methods

The pot experiment was conducted in two sets in the net house of the Department of Plant Physiology, College of Agriculture, Bhubaneswar, Odisha. The initial experiment included eighty pots, arranged according to a completely factorial randomized design (FCRD) with two replications. Eight chilli genotypes (five released varieties and three local landraces) were used: V1: BC-28, V2: Barkote, V3: Deogarh (local), V4: Utkal Ava, V5: Kenduguda (local), V6: Daringbadi (local), V7: Utkal Ragini and V8: Utkal Rashmi. Five water treatments were applied for 0hr, 6hr, 12hr, 18hr and 24hr. The good seedlings were transplanted at 30DAS following all management practices and were monitored regularly. The water treatment was imposed on the plants at 35DAT and water stagnation was maintained up to 2cm above soil and root level to the entire period of water logging to plants as per the above treatment details. Complete de-watering was carefully done from base hole of the pots after the stress imposition period was completed. The plants responses to water logging were monitored regularly upto 15 days after de-waterlogging and different adaptability screening scoring were recorded.

Individual plants were evaluated for wilting effects using a modified 0-5 scale from (4) (where 0 indicates a dead plant, 1; 75-100 % wilting from tip to base, 2; 50-74 % wilting from tip to middle, 3; undulating leaves between base and middle, 4; recurved leaf margins and 5; a green plant with no signs of wilting). Adventitious root formation (ARF) under waterlogging was assessed visually using a 0-3 scale from (5) (where 0 indicates no ARF, 1; low, 2; medium, 3; high and yellow leaf). The percentage of yellow leaves was determined using a 1-6 scale from (6) (where 1 indicates no yellow leaves, 2; 10-30 % yellow leaves, 3; 30-50 % yellow leaves, 4; 50-70 % yellow leaves, 5; mostly yellow leaves and 6; all leaves yellow). The second pot experiment was conducted in the same condition as the previous one, keeping a view of the same soil status and application of soil quantity, soil type and use of NPK and FYM. The selected two genotypes were treated with five water treatments (0 hr, 2 hr, 4 hr, 6 hr and 8 hr) and were replicated four times in a factorial completely randomized design and arranged in forty (40) numbers of pots. Each variety has one control i.e., Vo (no stress condition) given. The waterlogging duration was reduced from that of the first screening test as the mortality rate of death is high and we found difficulty in analyzing physiological and enzyme-related studies. The 30-day-old seedlings were transplanted in pots and when they attained 45 DAT, they were put under waterlogging conditions with standing water of 2 cm above soil and root level.

ROS and scavenging enzyme analysis

After waterlogging was alleviated, the recovery percentage and other experimental data, such as ROS levels and scavenging enzyme activities, were examined at 7-day intervals over three consecutive weeks. This analysis followed the established protocols for scavenging assays O_2^- (7), H_2O_2 (8) and enzymes, including Catalase (CAT (EC 1.11.1.7)), Peroxidase (APX (EC 1.11.1.7)), Superoxide Dismutase (SOD (EC 1.15.1.1)), Ascorbic Acid oxidase (AAO (EC 1.10.3.3)), Glutathione Peroxidase (GPOX (EC 1.11.1.9)) and Glutathione Reductase (GR (EC 1.6.4.2)). Calculation for Scavenging (or inhibition rate) (%) of O_2^- and H_2O_2= $(1-A_1 -A_2)/A_0)\times100$ where A2= Abs without reagent. A_0= Abs of control (without extract), A1=Abs with extract. The enzyme activity was calculated as (U/Min/g FW)= Change in abs./min × total reaction volume (mL) × total volume of enzyme extract × 1000 per Extinction Coefficient × volume of enzyme extract × fresh weight of tissue. The plants were properly maintained to collect yield and harvest related data. The data recorded were analysed using CropStat7.2 software downloaded from the internet and Microsoft Office Excel 2019-unit operating system as per (9).

Results and Discussion

After the waterlogging period ended, the individual plants were evaluated for tolerance (Fig-1). Observations from 7 to 21 days showed that Barkote and Daringbadi had a low number of adventitious roots and a 10-50 % yellow leaf percentage compared to other genotypes, which had 50-100 % damage. Consequently, Barkote and Daringbadi were chosen for further study. The genotypes Barkote and Daringbadi was chosen for further study in second set of experiment to evaluate the physiological alteration that occurred when exposed to waterlogged conditions. It was observed in the screening test that the survival percentage was meagre when plants were exposed to waterlogging conditions more than 12 h. Therefore, a modified treatment of waterlogging situations like 0 hr, 2 hr, 4 hr, 6 hr and 8 hr was applied to understand the scavenging enzyme activity due to the outburst of reactive oxygen species(ROS) in the chilli plant.

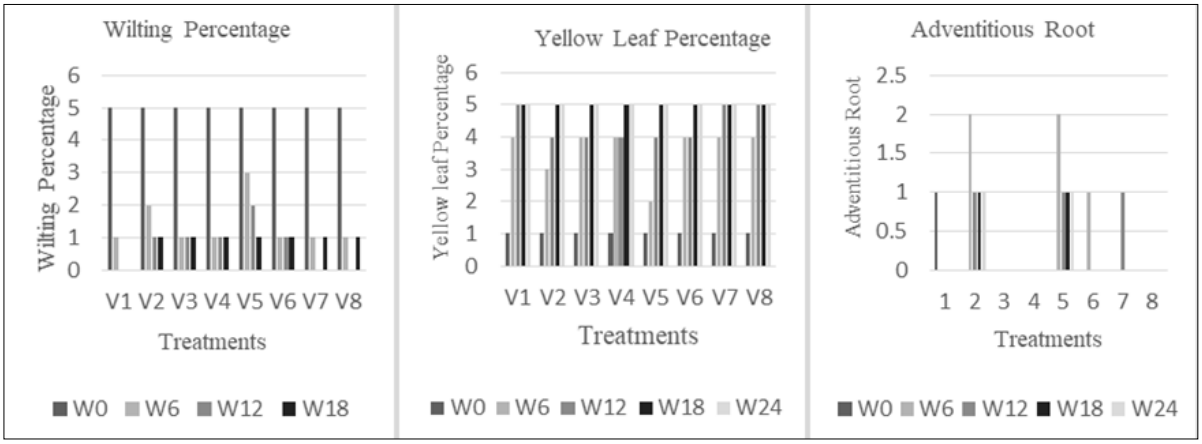

Fig. 1. Effect of waterlogging on wilting, yellowing percentage and adventitious root formation of chilli.

Physiological effect of waterlogging on chilli plant

Leaf was found to be the most sensitive organ during waterlogging in chilli. There is a change in leaf colour up to 60 days of de-waterlogging, but thereafter, the plant regains and has strong adaptability. We found that after de-waterlogging the leaves of the treated chilli varieties turned yellow and sometimes deep green and can recover independently. Similar findings indicated that root hypoxia disrupts substance transport and directly affects plant morphology, leading to leaf discolouration, wilting, or leaf drop (10).

Effect of waterlogging on Malondialdehyde (MDA) levels in chilli plant

The MDA activity was measured to determine the extent of Lipid peroxidation among treated and untreated plants. MDA concentration relatively increased at a high rate in 2 hr of water stagnation in both the varieties and thereafter, it declined at 4 hr of water stagnation and again, MDA activity increased at 6 and 8 hr of water treatment (Fig. 2). MDA activity was maximum at 6 hr of water treatment in both the genotypes, which might cause higher lipid peroxidation in comparison to other treatments. The accumulation gradually decreased as the periods of water stagnation increased in both the genotypes with a tune of 10.8 to 46.6 % than the control. The data showed statistically significant differences in varieties, treatments and their interactions.

Effect of waterlogging on ROS production in chilli plants

The reactive oxygen species like O_2^-, H_2O_2 generated during water stress available in leaf of each treatment was computed by percentage scavenging inhibition per 0.5mg/mL, 1mg/mL, 1.5mg/mL, 2mg/mL crude leaf extract (Fig. 3-4). The inhibition of O_2^- was increased to 10.3 % in Barkote and 9.7 % in Daringbadi after 2 hr of water stagnation under 0.5 mg/mL of assay. The percent inhibition of O_2^- was reduced to a minimum level at 8 hr of water stagnation in 0.5 to 2 mg/mL assay in Barkote and Daringbadi except increased trend was observed in Daringbadi at 2mg/mL assay. The percentage inhibition of H_2O_2 was increased to a level of 65.1 %, 40.1 % and 47.3 % in Daringbadi, after 2 hr of water stagnation under 0.5 mg/ml of assay except decreased trend observed under 1.5 mg/mL over their respective control. The inhibition of H_2O_2 showed a percentage increased and decreased trend at 8 hr of water stagnation in 0.5, 1.0 and 2 mg/mL assay in Barkote and Daringbadi, except a decreased trend was observed at 1.5 mg/mL assay. Waterlogging leads to the accumulation of reactive oxygen species (ROS), resulting in increased membrane peroxidation and malondialdehyde (MDA) production, along with heightened activities of superoxide dismutase (SOD) and peroxidase. Our study observed increased ROS activity, which triggered an oxidative burst, as evidenced by elevated H_2O_2 and O_2^- levels. SOD is crucial in protecting cells from oxidative damage caused by ROS. In addition to its roles in photosynthesis and respiration, the extracellular matrix (ECM) significantly contributes to H_2O_2 production, which is vital for regulating plant growth, development, acclimation and defence mechanisms. During various environmental stresses, the highest concentrations of H_2O_2 are typically observed in the leaf veins (11). Thus, the scavenging system of susceptible plants (6 dead) of the first experiment was negatively affected.

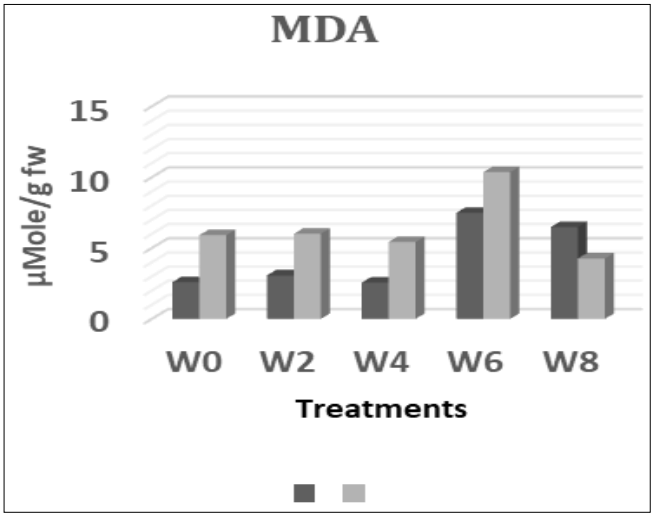

Fig. 2. Effect of waterlogging on MDA and elevated MDA after 10 days of de-waterlogging.

Effect of waterlogging on antioxidant enzyme in chilli

Our study found that the activities of catalase, peroxidase, SOD, glutathione peroxidase, glutathione reductase and ascorbic acid oxidase were initially high in the two local cultivars (Barkote and Daringbadi). However, these activities decreased after 10 days of de-waterlogging, reducing the capacity to remove H_2O_2 and an increased accumulation of H_2O_2. This accumulation further inhibited SOD activity and increased O_2^- levels, particularly in the local chilli variety Daringbadi. Elevated H_2O_2 levels can also generate harmful radicals, contributing to lipid peroxidation, plant wilting and, ultimately, plant death. The reduction in SOD and GR activities under waterlogging differed between the cultivars, with Barkote showing the most significant decrease and Daringbadi the smallest, suggesting varying levels of resistance to waterlogging. Our results indicate that elevated H_2O_2, O_2^- and MDA levels indicate oxidative stress. The mean value of catalase activity was found high in Daringbadi (13.7 µM/mg protein/min) than in Barkote (8.2µM/mg protein/min) with a tune of 40.1 % high than the later (Table 1). Their interaction and sole action over variety and waterlogging were statistically significant. The peroxidase activity per min was decreased in Daringbadi at 30 days of de-waterlogging (DAD) over their respective controls. Glutathione peroxidase (GPX) activity per min was decreased in Barkote and increased in Daringbadi to the duration of waterlogging from 2 hr to 8 hr. The mean value of GPX activity in Barkote was 0.32µM/mgprotein/min and Daringbadi was 0.65µM/mg protein/min. SOD percentage inhibition was increased in Daringbadi and decreased in Barkote and increased in Barkote to the duration of waterlogging from 2 hr to 8 hr over their respective controls. The glutathione reductase activity per gm FW to degrade NADH per gm FW was high in Barkote and Daringbadi at 4 hr and 6 hr, whereas shown low in Barkote and Daringbadi at 2 hr and 8 hr than their respective control. The mean value of ascorbic acid oxidase was found high in Barkote (2.89µM/mg protein/min) than in Daringbadi (1.76µM/mg protein/min) with a tune of 39.1 % high than the later. Their interaction and sole action over variety and waterlogging was statistically significant and negatively correlated with yield (p<0.01). When the levels of antioxidants such as catalase (which neutralizes H_2O_2 produced during

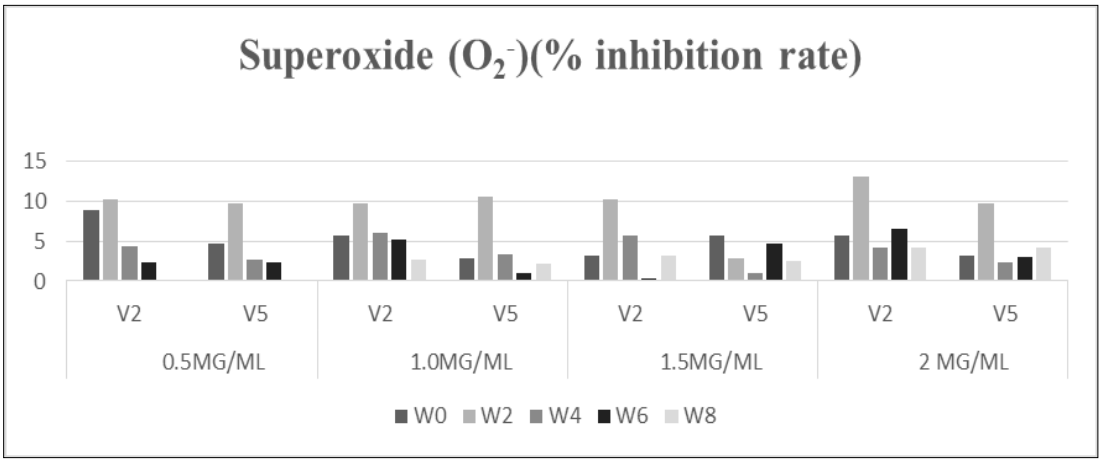

Fig. 3. ROS activity that leads to the oxidative burst as evidenced by the elevated levels of O_2^-.

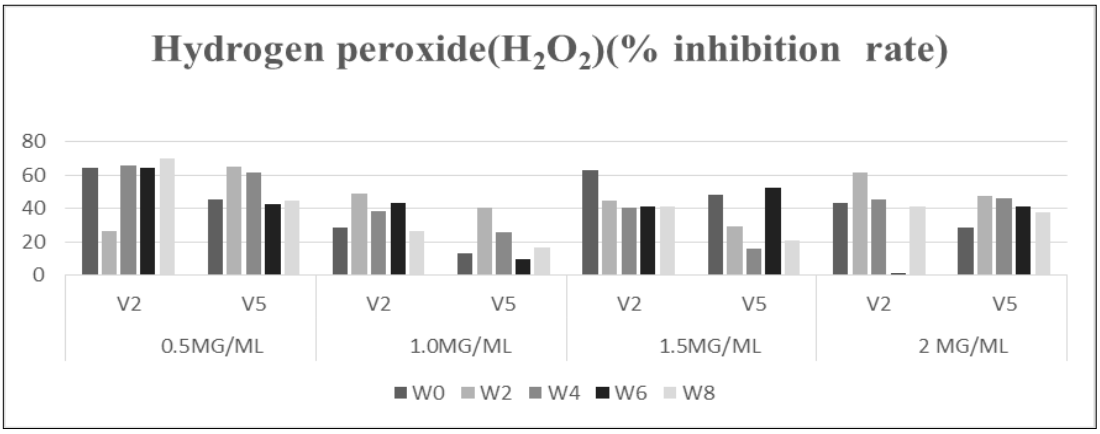

Fig. 4. ROS activity that leads to the oxidative burst as evidenced by the elevated levels of H_2O_2.

Table 1. Catalase, peroxidase, sod, gluathione peroxidise, glutathione reductase and ascorbic acid oxidase activities of the two selected local cultivars (Barkote and Daringbadi)

Treatments	CAT (µMole/mg protein/min)	APX µMole/mg protein/ min	GR µMole NADPH/mg protein/min	GPX (µMole/mg protein/min)	AAO µMole/mg protein/ min	SOD µMole/mg protein/min
Barkote- 0hr	4.95	53.28	0.16	0.67	1.00	0.37
Barkote-2 h	10.96	138.81	0.14	0.39	1.07	0.18
Barkote-4 h	16.23	111.51	0.76	0.26	0.76	0.30
Barkote-6 h	0.12	65.44	0.42	0.18	1.86	0.14
Barkote-8 h	8.92	13.99	0.13	0.08	9.79	0.36
Daringbadi-0hr	0.35	167.00	0.34	0.04	0.24	0.20
Daringbadi-2 h	12.74	122.92	0.09	0.10	0.45	0.59
Daringbadi-4 h	17.76	105.22	0.54	1.02	2.84	0.21
Daringbadi-6 h	18.43	373.20	0.23	1.37	1.79	0.52
Daringbadi-8 h	19.10	4.08	0.21	0.74	3.48	0.58
Sem(±)						
V	0.29	0.22	0.02	0.01	0.07	0.02
W	0.46	0.35	0.04	0.03	0.12	0.03
V×W	0.65	0.50	0.05	0.04	0.17	0.05
CD(0.05)						
V	0.86	0.67	0.08	0.06	0.23	0.07
W	1.36	1.06	0.12	0.09	0.36	0.11
V×W	1.92	1.50	0.17	0.12	0.51	0.15

V- Variety; W- Waterlogging treatment; CD- Critical difference

mitochondrial electron transport and is crucial for plant defence, ageing and senescence), peroxidase (which reduces peroxides and generates reactive oxygen species), SOD (which is essential for physiological defence against free radicals and ROS), glutathione peroxidase (which shows varying tissue-specific expression patterns), glutathione reductase (which is involved in both enzymatic and non-enzymatic redox reactions within the cell) and ascorbic acid oxidase (which regulates the redox state, cell wall metabolism and cell expansion and affects cell wall loosening) are significantly lower compared to ROS levels in treated plants, it may trigger the cell death pathway, leading to senescence and death of plant. Research suggests that stress-induced declines in photosynthesis can lower NADPH demand in the Calvin cycle, reducing the photosynthetic electron transport chain. This disruption in function subsequently leads to the production of reactive oxygen species (12).

Effect on yield in chilli

Under control conditions, the maximum number of fruits [36] was recorded in Barkote (Table 2). However, there was a considerable decrease in fruit numbers concerning waterlogging. In Barkote, there was a % drop of 27.7 %, 38.8 %, 58 % and 77.7 % after 2, 4, 6 and 8 hr of waterlogging, respectively. Barkote had the least number of fruits (8) after 8 h of waterlogging, followed by Daringbadi [10]. The interaction between variety and treatment was statistically significant and positively correlated with fruit yield (p<0.01). The maximum number of seeds per fruit was recorded in Barkote [31] under control conditions. Still, there was a significant decrease in seed numbers in the different periods of waterlogging, ranging from 12.9 % to 70.9 %. Barkote had the maximum fruit weight of (1.37g), than the various periods of waterlogging treatment, where the fruit weight sharply decreased with a range varying from 11.6 % to 74.4 %. Studies have shown that short-term waterlogging at 45 days after transplanting (DAT) in Kharif tomatoes significantly reduces yield and components. In line with these findings, our study also demonstrates that waterlogging during the early growth stage severely impacts chilli fruit yield. Waterlogging adversely affects key yield components of chilli, such as the number of fruits per plant and the average fruit weight. Data from our experiment revealed that waterlogging at 45 DAT led to a substantial decrease in fruit number and total yield in local cultivars, similar to the reduction in fruit number per plant observed in tomatoes under short-term waterlogging (13). This reduction in fruit number was accompanied by decreased fruit length and girth. Additionally, the drop in fruit yield was associated with increased shoot biomass production. This suggests that the Daringbadi variety may allocate less energy to vegetative growth than fruit production, consistent with the findings of (14).

Conclusion

The findings of this study unequivocally indicate that waterlogging exerts adverse effect on the growth, development and productivity of chilli plants. Notably, plants subjected to root hypoxia for durations ranging from 12 to 24 hr suffered mortality, except for Barkote and Daringbadi varieties, which displayed resilience by surviving up to 12 hr of water stagnation. As waterlogging persisted, the metabolic activity of the plants showed a significant decrease after 8 hr, compared to the 6-hr mark. Moreover, the impact of waterlogging stress was clearly evident in the reduction of yield. Nevertheless, despite these formidable challenges, the Barkote variety outperformed others in all aspects and exhibited some resistance to stress by adapting its mechanisms to regulate scavenging enzymes in response to root hypoxia that cause outbursts of ROS.

Acknowledgements

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Authors' contributions

RP conceived the study. RKP, PB, RKN and PT designed the experiment. PB carried out the experiments and recorded observations; RP and PB did tissue tolerance assay and enzyme estimation; RP and PB analyzed the data and drafted the manuscript; all the authors reviewed and approved the manuscript.

Table 2. Effect of waterlogging on yield of chilli

Treatments	No of fruit/ plant	Fruit length (cm)	Fruit girth (cm)	Pedicle length (cm)	No of seeds/plant	Average fruit weight (g)	Yield /plant (g)
Barkote- 0 h	36.00	3.10	1.4	2.80	31.00	1.37	49.32
Barkote-2 h	26.00	2.90	1.1	2.40	27.00	1.21	31.46
Barkote-4 h	22.00	2.50	0.8	2.10	21.00	1.09	23.98
Barkote-6 h	15.00	1.90	0.6	1.60	19.00	0.67	10.05
Barkote-8 h	8.00	1.10	0.3	1.10	9.00	0.35	2.8
Daringbadi-0 h	30.00	3.00	1.2	2.60	29.00	1.27	38.1
Daringbadi-2 h	21.00	2.60	0.9	2.10	18.00	1.11	23.31
Daringbadi-4 h	16.00	2.30	0.7	1.80	14.00	1.01	16.16
Daringbadi-6 h	16.00	1.70	0.5	1.50	13.00	0.76	12.16
Daringbadi-8 h	10.00	1.30	0.3	1.20	10.00	0.45	4.5
Sem(±)							
V	0.56	0.06	0.02	0.05	0.43	0.01	0.52
W	0.88	0.10	0.03	0.09	0.69	0.02	0.83
V×W	1.25	0.14	0.04	0.12	0.97	0.04	1.18
CD(0.05)							
V	1.65	0.20	0.06	0.17	1.29	0.05	1.56
W	2.61	0.31	0.09	0.27	2.04	0.08	2.46
V×W	3.69	0.44	0.13	0.38	2.88	0.12	3.49

V- Variety; W- Waterlogging treatment; CD- Critical difference

Compliance with ethical standards

Conflict of interest: The authors declare no conflict of interest concerning this manuscript.

Ethical issues: None

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