

Review Article

Phytoprotectants in action: Shielding plants from oxidative damage under temperature extremes and waterlogging stress

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ABSTRACT

Waterlogging (WL) and extreme temperatures are major abiotic stresses that threaten agricultural productivity. High and low temperatures impair photosynthesis, reduce enzyme activity and destabilize membranes, whereas WL causes hypoxia, nutrient imbalance and metabolic disorder. Both stresses lead to excessive build-up of reactive oxygen species (ROS), and the resulting oxidative stress damages lipids, proteins and nucleic acids, reducing plant growth and yield. Reactive oxygen species are natural byproducts of plant metabolism, but their rapid increase during stress disturbs redox balance, destabilizes cellular structure and can cause irreversible damage or even plant death. Naturally occurring or synthetic phytoprotectants applied exogenously have therefore been studied extensively for their ability to improve plant tolerance. These compounds include antioxidants, osmoprotectants, phytohormones, biostimulants and plant extracts, and they increase stress resistance by enhancing enzymatic and non-enzymatic antioxidant defense, stabilizing membranes, regulating stress-responsive genes and maintaining osmotic balance. In temperature-stressed plants, compounds such as salicylic acid, ascorbic acid and brassinosteroids alleviate heat- or cold-induced oxidative damage, while under WL, ethylene synthesis inhibitors, polyamines and signaling molecules improve redox balance and sustain metabolism. This review summarizes recent evidence on how phytoprotectants mitigate oxidative stress under extreme temperatures and WL and discusses their potential for climate-resilient crop production.

Introduction

Climate change has reduced environmental services and made plants more vulnerable to multiple abiotic stresses throughout their growth and development. Abiotic stresses, including heat, chilling, water deficit, waterlogging (WL), salinity, nutrient imbalance, heavy metal toxicity and xenobiotics (pesticides and fertilizers), cause about 50% of

global crop yield loss (Saini et al., 2018). Extreme temperatures, excess irradiation, irregular rainfall, storms and accumulation of toxic elements in soil are interconnected and contribute to these stresses (Bhuyan et al., 2020).

Plants exposed to extreme temperatures suffer cellular and physiological damage due to

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overproduction of reactive oxygen species (ROS). Excessive ROS alter membrane lipids, denature proteins and disrupt enzymatic activity, leading to the breakdown of cellular structure (Shah et al., 2019). Heat shock proteins (HSPs) and various signaling genes contribute to heat tolerance, whereas chilling and freezing injury largely results from loss of membrane integrity due to lipid solidification. Osmoprotectants such as proline (Pro), glycine betaine (GB) and sugars help plants achieve cold acclimation. Waterlogging deprives roots of oxygen, and the resulting hypoxic or anoxic conditions cause cellular damage through excessive ROS production (Huo et al., 2022). To avoid such damage, plants regulate ROS through a complex network of enzymatic and non-enzymatic antioxidants.

Commercial phytoprotectants and biostimulants are emerging agronomic tools with a rapidly growing market and complex formulations derived from organic, inorganic or microbial sources. Bioactive compounds, including seaweed extracts, amino acids, polyamines (PAs), phytohormones, melatonin, nitric oxide (NO) donors and beneficial soil microbes, activate ROS detoxification pathways by improving antioxidant activity, enhancing the accumulation of protective osmolytes and improving water and nutrient uptake. They also promote root growth, photosynthesis and pigment content, thereby sustaining growth and productivity under extreme temperature and WL. Because stress tolerance involves integrated physiological, biochemical and molecular responses, understanding the interaction between ROS production, antioxidant defense and phytoprotectant action is essential for sustainable crop production under stress conditions.

Although many studies have reported beneficial effects of exogenous phytoprotectants under individual abiotic stresses, the evidence for extreme temperatures and WL remains scattered across crop species, compounds, doses and experimental conditions. This makes it difficult to identify common protective mechanisms. We hypothesize that phytoprotectants improve plant tolerance to high

and low temperatures and WL mainly by limiting ROS overproduction and strengthening enzymatic and non-enzymatic antioxidant defenses. They also maintain membrane stability, osmotic balance and photosynthetic performance. To test this hypothesis, this review first summarizes how extreme temperatures and WL disturb plant physiology and trigger oxidative stress, and then outlines ROS generation and antioxidant defense in plants. It further classifies the major phytoprotectants and their modes of action, and evaluates recent evidence on phytoprotectant-mediated mitigation of oxidative damage under high temperature, low temperature and WL.

Plant responses to extreme temperature and waterlogging

Global warming is increasing soil and air temperature, and a rise of around 2–3 °C is anticipated by 2050 (Quintero-Calderon et al., 2021). High temperatures can cause serious yield loss and accelerate food insecurity (Yu et al., 2024). Many biochemical reactions in plants are highly sensitive to temperature, and protein and enzyme activity are strongly influenced by rapid increases in soil or air temperature (Kul et al., 2020). Deviation of about 10–15 °C above or below the optimum temperature causes heat or chilling/freezing stress, leading to excessive ROS production that disrupts metabolism and damages critical cellular components (Bita and Gerats, 2013). Under heat stress, photosynthetic quantum efficiency and enzyme activities decrease, while HSP synthesis and calcium (Ca^{2+}) influx increase to mediate stress responses (Bita and Gerats, 2013). Heat stress (35 °C) increased superoxide ($\text{O}_2^{\cdot-}$) content by 79.9% in cucumber (Ding et al., 2016), and in field-grown sorghum, high temperature raised $\text{O}_2^{\cdot-}$ content 3.5-fold in pollen and 2.3-fold in pistils (Djanaguiraman et al., 2018).

When temperature falls below the optimum range, metabolic activity slows, and physiological responses are delayed (Kul et al., 2020). Low temperature

retards root growth and lateral root development and reduces water and nutrient uptake. It also increases oxygen solubility and accumulation and promotes electron leakage from the electron transport chain (ETC), causing ROS overproduction that affects membrane fluidity and the photosynthetic apparatus (Jalil et al., 2017). Chilling reduced chlorophyll (Chl) content and tissue water status in cucumber seedlings (Zhang et al., 2012), while in tomato, low temperature increased malondialdehyde (MDA) content, *RBOH1* expression and accumulation of hydrogen peroxide (H_2O_2) and $O_2^{\cdot-}$ (Liu et al., 2018). Cold-stressed rice seedlings showed a 180% rise in MDA content and a 49% rise in electrolyte leakage (EL; Han et al., 2017).

Excess soil water from heavy rainfall and poor drainage creates hypoxic or anoxic conditions, affects nearly 10% of the world's land and causes significant yield loss. Oxygen diffusion in waterlogged soil is about 10,000 times slower than in air, which inhibits root respiration, promotes ROS accumulation and disturbs physiological processes (Loreti et al., 2016; Yamauchi et al., 2019). Low oxygen inhibits the ETC in chloroplasts and mitochondria, leaches essential nutrients and increases heavy metal availability (Steffens, 2014). Waterlogging also causes stomatal closure, Chl degradation, wilting and leaf senescence (Arbona et al., 2017). In sesame, oxygen deprivation elevated lipid peroxidation and ROS (Anee et al., 2019), and a WL-sensitive sorghum accumulated more MDA than a tolerant one (Zhang et al., 2019b).

Reactive oxygen species and antioxidant defense in plants

Reactive oxygen species are an unavoidable consequence of aerobic metabolism. Chloroplasts, mitochondria and peroxisomes, which have highly oxidizing metabolism or an intense rate of electron flow, are the major sources of ROS in plant cells (Dmitrieva et al., 2020). Chloroplasts are particularly susceptible because they are rich in

photosensitizers such as Chl and in polyunsaturated fatty acids (Fig. 1). If excess light energy is not quenched efficiently, triplet-state Chl transfers energy to ground-state oxygen (3O_2), producing highly reactive singlet oxygen (1O_2 ; Dmitrieva et al., 2020). Ground-state oxygen can also accept electrons from the photosynthetic ETC or NADPH oxidase to form $O_2^{\cdot-}$, which reacts with protons to produce the hydroperoxyl radical ($HO_2^{\cdot}$; Hasanuzzaman et al., 2019a). Hydrogen peroxide is produced spontaneously or enzymatically through dismutation of these radicals by superoxide dismutase (SOD), peroxidase (POD) and NADPH oxidase (Rejeb et al., 2015), and the highly reactive hydroxyl radical ($\cdot OH$) forms through metal-catalyzed Fenton reactions between ferrous ions and H_2O_2 (Demidchik, 2015). Cellular ROS therefore include both free radicals and non-radicals (Maurya, 2020). In non-green tissues, mitochondria are the main source of ROS through electron leakage from complexes I and III of the ETC, while peroxisomes produce H_2O_2 during photorespiration and fatty acid oxidation (Singh et al., 2019).

At low or moderate concentrations, ROS act as signaling molecules, but under severe stress, excess ROS cause lipid peroxidation, protein oxidation, damage to the photosynthetic machinery and programmed cell death. Plants balance ROS through non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), α -tocopherol, carotenoids and flavonoids, and enzymatic antioxidants such as SOD, ascorbate peroxidase (APX), catalase (CAT), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR) and glutathione reductase (GR; Laxa et al., 2019). Enzymatic antioxidants catalyze ROS conversion and removal, whereas non-enzymatic antioxidants interrupt free-radical chain reactions and support cellular redox homeostasis (Hasanuzzaman et al., 2019b).

Antioxidant capacity under stress varies among species and genotypes. In chickpea (*Cicer arietinum*), a heat-sensitive genotype showed suppressed APX and GR activity with elevated H_2O_2 , whereas a

tolerant genotype enhanced antioxidant activity and maintained ROS levels (Kumar et al., 2013). In heat-stressed germinating rice seeds, SOD and CAT activities and the expression of *OsSOD*, *OsPOD*, and

(Zhao et al., 2016), and chilled rice seedlings increased SOD and CAT activities, along with the GSH to oxidized glutathione (GSSG) ratio (Han et al., 2017). Under WL, sesame plants showed lower

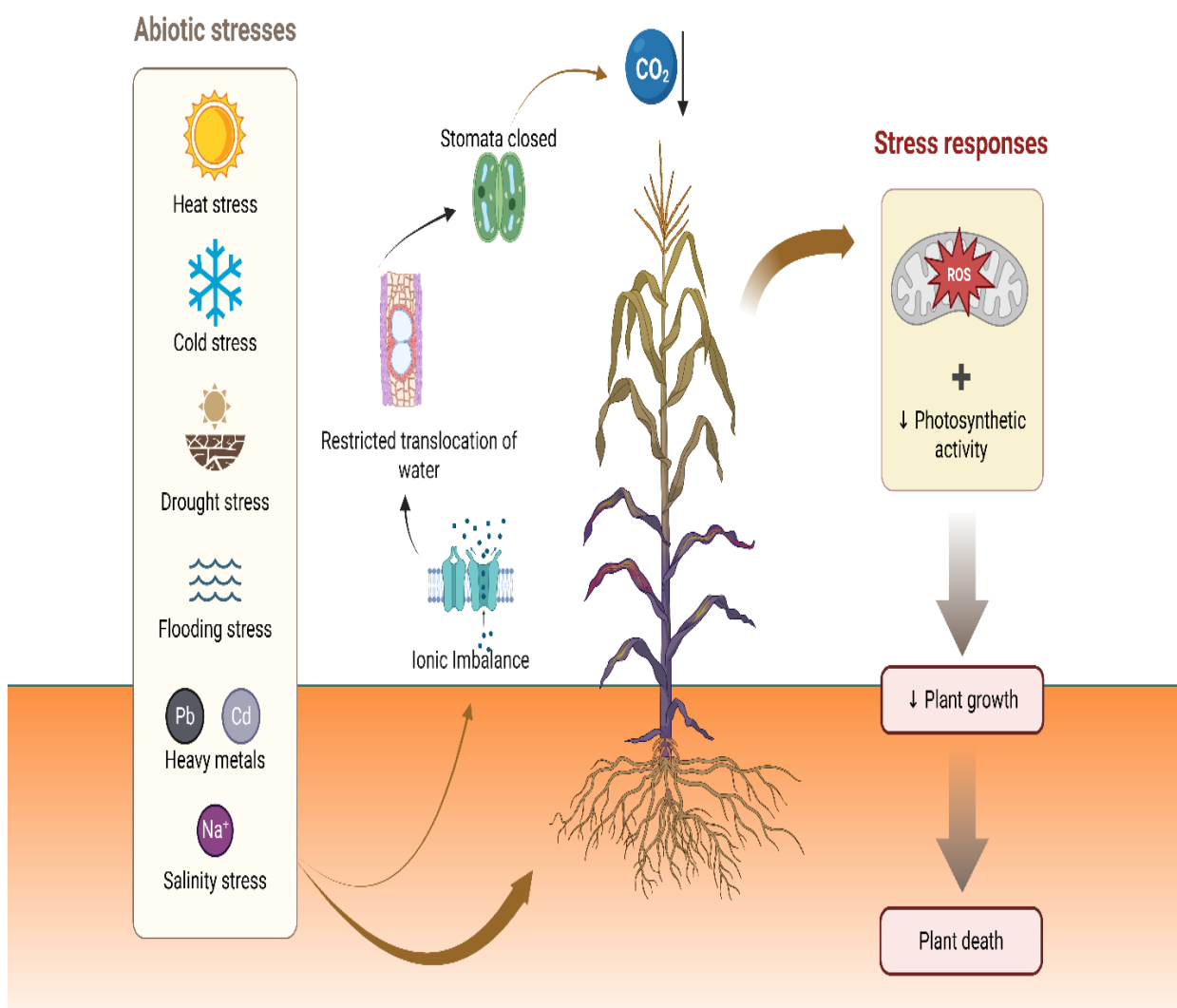


Fig. 1. Abiotic stresses and reactive oxygen species-mediated physiological responses in plants.

OsCAT were suppressed (Liu et al., 2019), whereas priming boosted SOD and CAT activity in cotton (Sarwar et al., 2018), and treatment with the hydrogen sulfide (H_2S) donor sodium hydrosulfide (NaHS) upregulated AsA and GSH biosynthesis and antioxidant enzyme activity in strawberry (Christou et al., 2014). Under low temperature, cucumber seedlings showed 3-fold and 2-fold increases in Cu/Zn-SOD and Fe-SOD activities, respectively

but higher GSH and GSSG contents, with increased APX and MDHAR but decreased DHAR and GR activities (Anee et al., 2019). In maize, WL increased SOD activity by 19–57%, POD activity by 19–107% and CAT activity by 26–57% across genotypes (Li et al., 2018). The antioxidant system is therefore central to stress tolerance, but it is often insufficient under severe stress, which is why phytoprotectants are applied exogenously.

Phytoprotectants in action

Abiotic stresses reduce both the quantity and quality of crop yield. To limit such negative effects, plants use a set of phytoprotectants, natural substances and processes that increase stress tolerance and preserve cell integrity (Fig. 2). Among them, phytohormones coordinate complex stress responses. Absciscic acid (ABA) regulates adaptation to drought, salinity and temperature extremes by closing stomata, triggering seed dormancy and mediating the transcription of stress-responsive genes. Absciscic acid also interacts synergistically or antagonistically with gibberellins, auxins, cytokinins, salicylic acid (SA), jasmonic acid, ethylene, brassinosteroids (BRs) and strigolactones, maintaining a well-regulated hormonal balance under stress (Singh and Roychoudhury, 2023; Zheng et al., 2023; Das et al., 2025).

Beneficial microbes, including endophytes and plant growth-promoting rhizobacteria (PGPR), provide

further phytoprotection by stimulating nutrient uptake, producing phytohormones and antioxidants and activating stress signaling pathways (Singh et al., 2023; Ameen et al., 2024; Kumar et al., 2025). Arbuscular mycorrhizal fungi (AMF) enhance water and nutrient uptake, especially under salt and drought stress (Acosta-Motos et al., 2020; Munir et al., 2022). Enzymatic (SOD and CAT) and non-enzymatic (AsA and GSH) antioxidants scavenge stress-induced ROS (Parvin et al., 2022; Zheng et al., 2023), and phenolic compounds act as both antioxidants and signaling molecules. Osmoprotectants such as Pro, GB, sugars and sugar alcohols stabilize proteins and membranes, maintain osmotic balance and modulate stress-responsive genes (Acosta-Motos et al., 2020). Together, these phytoprotectants form an integrated defense system that helps plants survive and adapt to unfavorable environments.

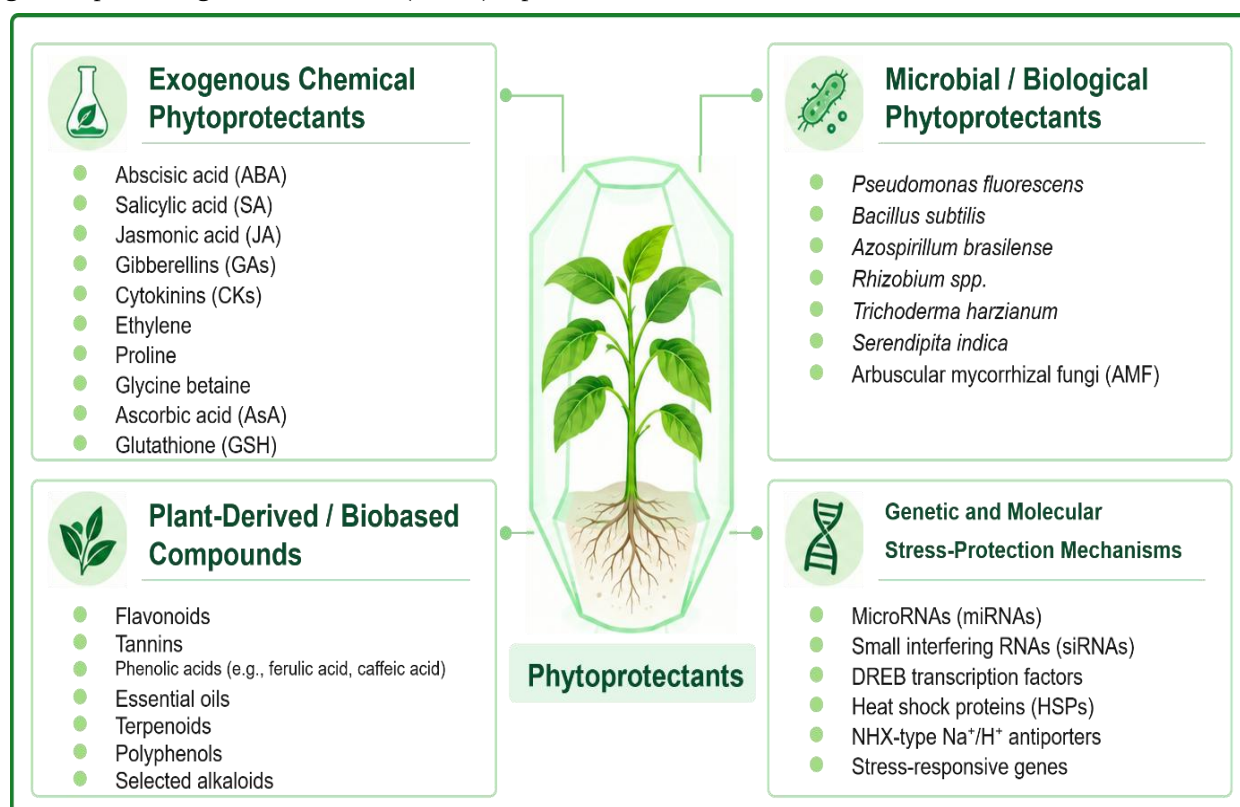


Fig. 2. Types of chemical, biological, and plant-derived phytoprotectants and genetic approaches for plant stress mitigation.

Phytoprotectants for improving plant tolerance to temperature extremes and waterlogging

High temperature

Besides ROS, heat stress generates methylglyoxal, a cytotoxic compound that modifies DNA and proteins (Kaur et al., 2016). Heat affects all growth stages from germination to maturity, causing poor germination, stunted vegetative growth and drying of inflorescences. Plants counter these effects by producing protective solutes, activating enzymes and altering gene expression to maintain cell homeostasis, water balance and antioxidant defense (Rao et al., 2025). Biostimulants contain bioactive molecules that regulate primary and secondary metabolism and increase the capacity of plants to face adverse climatic conditions (Bulgari et al., 2019), and many have been applied exogenously to improve high temperature tolerance (Table 1). Because high-temperature often occurs together with water deficit and osmotic stress, the underlying protective mechanisms are complex.

Phytohormones and signaling molecules are among the most widely tested. Foliar BRs improved stomatal conductance, photosynthetic pigments, ion contents and biochemical parameters of rice under high temperature across different phenological stages (Pantoja-Benavides et al., 2022), probably because BRs increase photosynthetic carbon fixation and regulate stomatal function and pigment content (Siddiqui et al., 2019). In rice seedlings at 40 °C, BRs, amino acids (AA), nitrophenolates (NP) and botanical extracts (BE) all reduced lipid peroxidation and lowered Pro content by about 22% (BRs), 34% (AA), 33% (BE) and 42% (NP) (Quintero-Calderon et al., 2021). Nitric oxide, ABA and melatonin have also shown additive benefits under high temperature in wheat and tomato. Nitric oxide improved photosynthesis and reduced EL; ABA induced osmolyte

accumulation and antioxidant enzyme activity and expression; and melatonin suppressed thermal damage by modulating PA and NO biosynthesis; all three reduced MDA and H₂O₂ and restored antioxidant activity (Jahan et al., 2019; Iqbal et al., 2022).

Melatonin is widely used as a biostimulant because of its high efficiency in ROS detoxification (Faizan et al., 2024). In tomato under combined salt and heat stress, 100 µM melatonin increased the electron transport rate, total antioxidant capacity and APX and GR activity, stabilizing membranes and reducing ROS generation (Martinez et al., 2018). Similarly, in wheat at 42 °C, 100 µM melatonin reduced lipid peroxidation and H₂O₂ accumulation, increased Pro biosynthesis, activated the AsA–GSH cycle through APX and GR and increased CAT, POD and SOD activity (Buttar et al., 2020).

Exogenous antioxidants and osmolytes are also effective. In wheat seedlings exposed to 33 °C for 6 d, GSH application, particularly at 0.5 mM, reduced MDA and restored shoot length, leaf area and Chl content, probably by protecting cell membranes against ROS (Suliman et al., 2024). In BT cotton under high temperature at squaring and flowering, 100 mg L⁻¹ selenium reduced H₂O₂, enhanced SOD, POD and CAT activity and improved Chl content, water relations and seed cotton yield (Saleem et al., 2020). In *Brassica napus* at 38 °C, 2 mM Pro and GB reduced H₂O₂ by 24% and 11%, respectively; Pro also reduced lipoxygenase (LOX) activity and MDA content, and both osmolytes enhanced the AsA–GSH pathway, antioxidant defense and glyoxalase system (Hasanuzzaman et al., 2020). In Chinese cabbage at 45 °C, 15 mM GB and 0.2 mM β-aminobutyric acid improved photosynthetic performance and reduced EL and MDA (Quan et al., 2022). A follow-up study of GB-primed Chinese cabbage showed that heat increased O₂^{•-} and reduced ATP and relative water content,

indicating impaired energy metabolism (Quan et al., 2023).

Polyamines act similarly. In rice exposed to 38–43 °C at flowering, 1.5 mM foliar spermidine (Spd) increased SOD, CAT, APX, and GPX activity by 16–43%, lowered H₂O₂ and MDA, and improving spikelet fertility and grain yield (Karwa et al., 2022). In tomato seedlings at 38/28 °C, 1 mM Spd reduced growth inhibition and improved Chl content, photosynthetic rate, stomatal conductance and transpiration by reprogramming transcriptomic and physiological processes (Peng et al., 2023).

Beneficial microbes provide another route to thermotolerance. In soybean at 40 °C, the endophytic bacterium *Bacillus cereus* SA1 limited the increase in MDA to 3.5-fold, compared with more than 4-fold in non-inoculated plants, increased APX activity 3–4-fold and SOD activity 3.1-fold, and raised GSH content by 129% (Khan et al., 2020a). In tomato at 37 °C, where high temperature increased MDA by 385%, both SA1 inoculation and humic acid reduced MDA and GSH and increased SOD and APX activity (Khan et al., 2020b). Arbuscularmycorrhizal fungi improve nutrient mineralization and water availability in the root zone, and they enhance tolerance to extreme temperatures and other stresses by improving water balance and stomatal regulation, regulating phytohormones and stress-responsive genes, increasing osmolytes and raising SOD, CAT and POD activity; their extensive hyphal networks also increase phosphorus and nitrogen uptake (Chowdhary and Songachan, 2025).

Soil amendments and natural extracts also mitigate heat-induced oxidative damage. Biochar, a carbon-rich material that improves soil microbial activity and water and nutrient holding capacity (Wang et al., 2019a), protected *Arabidopsis* from the 1.6-fold increase in MDA caused by high temperature at 50 °C (Kumar et al., 2021), consistent with the lower MDA and

higher antioxidant enzyme activity reported in biochar-treated *Phragmites karka* under drought and high temperature (Abideen et al., 2020). Fulvic acid, which has a high ion exchange capacity, reduced MDA and H₂O₂, increased ABA content by 53.5% and 28.5% after 6 and 12 h, respectively, and increased SOD, APX and glutathione S-transferase activity in soybean at 35 °C (Dinler et al., 2016). Seaweed extracts raise the synthesis of osmoprotectants and antioxidants and regulate ABA and SA levels through bioactive compounds such as betaines, cytokinins and polysaccharides (Mukherjee and Patel, 2020). *Ascomyces nodosum* extracts reduced MDA and membrane damage in *Brassica juncea* (Goyal et al., 2023) and improved stomatal conductance and CO₂ assimilation in soybean under high temperature (Repke et al., 2022).

Low temperature

Many phytoprotectants have shown protective effects under cold stress in different crop species (Table 1). Prolonged cold ruptures cell membranes and dislocates phospholipid layers and cold-induced ROS damage proteins, lipids, carbohydrates and DNA, which can ultimately cause cell death (Gill and Tuteja, 2010).

Salicylic acid confers freezing tolerance largely by upregulating antioxidant enzymes. Priming wheat with 100 µM SA under mild cold (6/2 °C) for 2 d improved tolerance to late-spring freezing down to –4 °C; primed plants showed higher SOD, CAT, POD, APX, and GR activity, higher AsA and GSH, upregulated *WRKY19*, *AOX1a*, *HSF3* and *HSP70*, and better chloroplast integrity, photosynthesis, biomass and grain yield (Wang et al., 2020). In rice under salinity, seed treatment with cold plasma (10 kV) combined with 2 mM SA priming at 15 °C improved germination, seedling growth, photosynthesis, antioxidant enzyme activity, and K⁺, Ca²⁺ and Mg²⁺ uptake and reduced ROS and MDA (Sheteiwy et al., 2019). Cold exposure can also prime SA-dependent defense: *Arabidopsis thaliana* held at 4 °C for 10 h showed elevated H₂O₂, callose deposition and SA-pathway gene

expression and greater resistance to *Pseudomonas syringae* pv. *tomato* DC3000 (Wu et al., 2019).

Brassinosteroids and jasmonates are also effective. In eggplant fruit stored at 1 °C, 15 µM 24-epibrassinolide kept MDA content about 66% lower than in untreated fruit and reduced POD and polyphenol oxidase (PPO) activity, limiting oxidative damage (Gao et al., 2015). In wheat seedlings at 4 °C, 1 µM methyl jasmonate enhanced photosynthesis, stabilized membranes, increased SOD, CAT, and POD activity and Pro accumulation, and upregulated the cold-regulated genes *WCS19*, *WCS120*, and *WCOR15* (Repkina et al., 2021). 5-Aminolevulinic acid, a plant growth regulator and Chl precursor, is another candidate against temperature stress, because chilling strongly inhibits Chl biosynthesis. In etiolated rice seedlings greened at 18 °C and 12 °C, chloroplast ultrastructure, enzyme activity and Chl accumulation were progressively impaired, with 12 °C causing underdeveloped thylakoids and undetectable photosystem proteins (Zhao et al., 2020).

Exogenous antioxidants and low doses of H₂O₂ can also induce short-term cold acclimation. Root priming with 0.5 mM AsA protected tomato seedlings from chilling at 4 °C for 7 h by enhancing CAT, APX, and GPX activity, increasing Pro, sugar and amino acid accumulation and restoring nutrient uptake, thereby reducing H₂O₂ and EL (Elkelish et al., 2020). Priming four pistachio rootstocks (UCB-1, Badami, Ghazvini and Kaleh-Ghouchi) with 100 mM H₂O₂ before chilling at 14/4 °C for 96 h increased photosynthetic pigments, soluble proteins, APX, PPO, CAT, and GPX activity and osmolyte accumulation, while reducing EL, MDA and other aldehydes (JamshidiGoharrizi et al., 2024).

Beneficial microbes are among the most studied cold-stressphytoprotectants.

Arbuscularmycorrhizal fungi improve mineral nutrition, water status and secondary metabolite production. Under low temperature, inoculation with *Claroideoglomus etunicatum* and *Funneliformis mosseae* reduced MDA by 33%

and increased APX, SOD and CAT activity (Pasbani et al., 2020), and a consortium of four AMF species increased protective molecules and activated antioxidant enzymes at 14/8 °C for 7 d (Liu et al., 2023). In rice, co-inoculation with mycorrhizal helper bacteria and AMF improved biomass, antioxidant enzymes, osmoregulation and the expression of photosynthetic and low-temperature tolerance genes (Shi et al., 2025).

Psychrotolerant bacteria also protect crops under low temperature and could support the development of chilling-tolerant cropping systems (Vega-Celedon et al., 2021). In maize at 4 °C, the PGPR *Lysinibacillus fusiformis* YJ4 and *L. sphaericus* YJ5, which solubilize phosphorus and produce indole-3-acetic acid, gibberellins and siderophores, improved germination, growth, pigment content and photosynthesis; they increased Pro, GB, sugars and SOD, CAT and phenylalanine ammonia-lyase activity, improved N, P, K and Ca uptake, and modulated hormone balance, with co-inoculation being most effective (Jha and Mohamed, 2023). In wheat grown at 5 °C in the Himalayan region, the phosphorus-solubilizing endophyte *Acinetobacter rhizosphaerae* EU-KL44 increased growth, SOD and GR activity, osmoprotectants and P, Fe and Zn uptake, reduced lipid peroxidation and increased yield by up to 35% (Kour and Yadav, 2023a). Similarly, inoculating barley seeds with *Serratia nematodiphila* EU-PW75 under night temperatures below 5°C improved growth, tillering, Chl content, osmolytes and SOD and GR activity while reducing lipid peroxidation (Kour and Yadav, 2023b).

Seaweed extracts increase antioxidant molecules such as Pro, polyphenols, flavonoids and carotenoids that protect cells against frost-related oxidative damage (Borella et al., 2023). Extracts rich in Zn and Mn enhanced root growth and limited chilling-induced leaf injury in maize by improving micronutrient status and antioxidant enzyme activity (Bradáčová et al., 2016).

Table 1. Protective role of phytoprotectants in plants under high and low temperature stress.

Crop	Temperature levels	Doses of protectants	Beneficial effects	Reference
A. High temperature stress				
<i>Valerianella locusta</i>	35 °C	Se (Na ₂ SeO ₄), 50 mg dm ⁻³	Increased APX, GPX and CAT activity and GSH content	Hawrylak-Nowak et al. (2018)
<i>Oryza sativa</i>	38–43 °C	Spd, 1.5 mM, foliar spray	Reduced H ₂ O ₂ and lipid peroxidation; enhanced SOD, CAT, APX, and GPX activity	Karwa et al. (2022)
<i>Solanum lycopersicum</i>	38/28 °C, 7 d	Spd, 1 mM	Enhanced growth, Chl content, stomatal conductance, transpiration rate and net photosynthesis	Peng et al. (2023)
<i>Glycine max</i>	35 °C, 2 h for 2 d	Fulvic acid, 2.0 mg L ⁻¹	Increased RWC and SOD, APX, and GST activity; reduced H ₂ O ₂ and MDA content	Dinler et al. (2016)
<i>Raphanussativus</i> var. <i>radculus</i> Pers.	35 °C, 27 d	Melatonin, 0, 11.6, 17.4, 29.0, 34.8 ,and 67.0 mg L ⁻¹	Reduced MDA content; increased APX, GR, SOD, POD, and CAT activity	Jia et al. (2020)
<i>O. sativa</i>	40 °C, 5 h for 15 d	BRs, amino acids, nitrophenolates and botanical extracts (1, 30, 15 and 15 mM, respectively)	Reduced lipid peroxidation and Pro content; increased heat tolerance coefficient	Quintero-Calderon et al. (2021)
<i>Brassica rapa</i> ssp. <i>pekinensis</i>	30 °C, 5 d	BRs and JA (50, 100 and 200 nM); SA (1, 2 and 4 mM); SNP (0.25, 0.50 and 1.00 mM)	Increased CAT and POD activity	Lee et al. (2019)
<i>S. lycopersicum</i>	35 °C	Melatonin, 100 µM	Increased APX, GR and GPX activity	Martinez et al. (2018)
<i>O. sativa</i>	40 °C, 6 h for 7 d	ABA (1, 10 and 100 µM); fluridone (10 and 100 µM)	Increased ATP level and SOD, POD, CAT and APX activity; reduced H ₂ O ₂ and MDA content	Rezaul et al. (2019)
<i>Spinacia oleracea</i>	30 °C; seeds primed for 6 h	Seaweed extract, 0.15, 0.30, 0.60, and 1.2% (1 g seed in 10 mL solution)	Reduced MDA and H ₂ O ₂ content	AnjosNeto et al. (2020)
<i>B. napus</i>	38/28 °C, 24 and 48 h	Pro and GB, 2 mM	Increased AsA and GSH levels and CAT, APX, MDHAR, DHAR, GST, GPX, Gly I and Gly II activity; reduced MG, MDA and H ₂ O ₂ content and LOX activity	Hasanuzzaman et al. (2020)
<i>B. juncea</i>	35 °C	<i>Ascophyllum nodosum</i> extract, 25% (w/v)	Reduced MDA content and membrane damage; increased photosynthetic rate and Chl content	Goyal et al. (2023)
<i>G. max</i>	40 °C	<i>A. nodosum</i> extract, 1 L ha ⁻¹	Increased stomatal conductance, transpiration rate, CO ₂ assimilation rate and carboxylation efficiency	Repke et al. (2022)

Crop	Temperature levels	Doses of protectants	Beneficial effects	Reference
B. Low temperature stress				
<i>O. sativa</i>	15 °C for 24 h in darkness	Cold plasma (10 kV) and SA priming (2 mM)	Enhanced germination vigor, photosynthetic efficiency and antioxidant enzyme activity; reduced ROS and MDA; improved nutrient uptake and ultrastructure	Sheteiwy et al. (2019)
<i>Arabidopsis thaliana</i>	4 °C, 10 h	Cold priming before inoculation with <i>Pseudomonas syringae</i> pv. <i>tomato</i> DC3000	Triggered SA-mediated immune priming; increased H ₂ O ₂ , callose deposition and expression of defense genes (<i>PR2</i> and <i>PR5</i>)	Wu et al. (2019)
<i>Triticumaestivum</i> cv. Moskovskaya 39	Cold hardening at 4 °C	SA pretreatment, 100 µM	Increased SOD, CAT and GPOD activity and Pro content; reduced MDA and H ₂ O ₂ ; upregulated <i>TaMnSOD</i> , <i>TaFeSOD</i> and <i>TaCAT</i> transcripts	Ignatenko et al. (2019)
<i>T. aestivum</i> cv. Yangmai 16	6/2 °C, 2 d	SA priming, 100 µM	Enhanced SOD, CAT, POD, APX and GR activity, AsA and GSH, and expression of <i>WRKY19</i> , <i>HSF3</i> , <i>HSP70</i> , and <i>AOX1a</i> ; improved chloroplast integrity, Fv/F _m , biomass and yield	Wang et al. (2020)
<i>O. sativa</i>	12, 18 or 28 °C, 48 h	Etiolated seedlings (6 d in dark) greened under 120 µmol m ⁻² s ⁻¹ light	At 18 °C, moderate inhibition of Chl synthesis and GSA-AT, Mg-chelatase and POR activity, looser grana and elevated ROS and MDA; at 12 °C, severe inhibition, near absence of Chl and PSI/PSII proteins, no thylakoid development and high oxidative damage	Zhao et al. (2020)
<i>Coriandrumsativum</i>	6 °C, 6 d	Asahi SL (synthetic) and Goëmar Goteo (A. <i>nodosum</i>), 0.1%, foliar spray	Reduced MDA, H ₂ O ₂ and EL; increased total antioxidant activity and total phenolic content	Pokluda et al. (2016)

Crop	Temperature levels	Doses of protectants	Beneficial effects	Reference
<i>S. lycopersicum</i>	4 °C, 7 h	AsA root priming, 0.5 mM	Enhanced CAT, APX and GPX activity, osmolyte accumulation and nutrient uptake; reduced oxidative damage; suppressed stress-induced expression of catalase and HSP genes	Elkelish et al. (2020)
<i>T. aestivum</i>	4 °C, 7 h	MeJA pretreatment, 1 µM	Stabilized photosynthesis and membranes; increased SOD, CAT and POD activity and Pro content; upregulated <i>WCS19</i> , <i>WCS120</i> and <i>WCOR15</i>	Repkina et al. (2021)
<i>Z. mays</i>	4 °C	Seed inoculation with PGPR <i>Lysinibacillus fusiformis</i> YJ4 and <i>L. sphaericus</i> YJ5	Enhanced germination, growth, photosynthetic pigments and photosynthesis; increased SOD, CAT and PAL activity and osmolytes (Pro, GB and sugars); improved membrane integrity; modulated hormones (increased ABA/ACC and auxin/gibberellin); increased N, P, K and Ca uptake; co-inoculation most effective	Jha and Mohamed (2023)
<i>T. aestivum</i>	5 °C (Himalayan chilling)	Inoculation with psychrotrophic P-solubilizing <i>Acinetobacter rhizosphaerae</i> EU-KL44	Improved shoot and root growth and biomass; increased SOD and GR activity and osmoprotectants (Pro, GB and sugars); reduced lipid peroxidation; improved P, Fe and Zn uptake; up to 35% higher yield	Kour and Yadav (2023a)
<i>Hordeum vulgare</i>	Day ~20 °C, night <5 °C	Seed inoculation with psychrotrophic <i>Serratia nematodiphila</i> EU-PW75 (~10 ⁷ cells mL ⁻¹ , 1 h soaking before sowing)	Improved shoot and root length, biomass, tiller and spike number, Chl content, osmolytes (Pro, GB and sugars) and SOD and GR activity; reduced lipid peroxidation	Kour and Yadav (2023b)
<i>Z. mays</i>	12–14 °C	<i>A. nodosum</i> extract	Increased SOD activity in roots and leaves and improved Zn and Mn availability	Bradáčová et al., (2016)
<i>Solanum lycopersicum</i> L.	4 °C	Brown seaweed extract	Increased carotenoids, flavonoids, tannins, Pro and polyphenols	Borella et al. (2023)

Crop species	Duration of waterlogging	Dose of protectants	Regulatory effects	Reference
<i>G. max</i> cv. Daewon	WL, 2 d	ETP, 50, 100 and 200 μ M, spray	Restored shoot GSH content but further decreased root GSH; 100 μ M ETP restored shoot GR activity, whereas 100 and 200 μ M ETP further reduced root GR activity	Kim et al. (2018)
<i>G. max</i> cvs. Daewon and Pungsannamu	WL, 6 h	NO donors SNP or CySNO, 250 μ M	Reduced WL-induced $O_2^{\cdot-}$ accumulation in Daewon; in Pungsannamu, SNP and CySNO reduced $O_2^{\cdot-}$ by 15% and 46%, respectively; both lowered the elevated GSH in Daewon, whereas CySNO increased GSH in Pungsannamu	Khan et al. (2019)
<i>Vigna angularis</i> (Willd.) Ohwi & H. Ohashi	WL, 14 d	AsA, 3 and 5 mM	Reduced WL-induced MDA and EL; reversed the WL-induced increase in GSH; restored SOD and CAT activity towards control levels	Ullah et al. (2017)
<i>Medicago sativa</i> L. cv. 55v48	WL, 10 d	Melatonin, 100 μ M, pretreatment	Leaf EL and MDA content reduced by 25% and 27%, respectively	Zhang et al. (2019a)
<i>Triticumaestivum</i> L.	WL, 5 d	AOA, 100 μ M, soil drench	Reduced MDA, H_2O_2 and EL; lower GSH content and SOD, CAT and POD activity than in WL-stressed plants	Rauf et al. (2021)
<i>V. radiata</i> cvs. HUM-16 (WL-tolerant) and HUM-12 (WL-susceptible)	WL, 7 d	PBZ, 10 and 25 mg L^{-1} , seed treatment and foliar spray	MDA reduced by up to 32% (HUM-16) and 42% (HUM-12); reduced H_2O_2 ; increased SOD and APX activity, more in the tolerant cultivar	Yadav and Hemantaranjan (2017)
<i>Elaeagnus angustifolia</i> L.	WL, 14 d	NaCl, 0.6%, soil drench	Further increased SOD, POD, APX and GR activity compared with WL alone	Liu et al. (2020)
<i>G. max</i> cv. AN 8500	WL, 32 d	H_2O_2 , 70 mM, pretreatment	In roots, H_2O_2 , $O_2^{\cdot-}$, MDA and EL reduced by 57%, 36%, 35% and 25%, respectively; in leaves, H_2O_2 , $O_2^{\cdot-}$ and MDA reduced by 46%, 96% and 11%, respectively; increased SOD, CAT and APX activity	Andrade et al. (2018)

Waterlogging

Compared with other major abiotic stresses, fewer studies have examined phytoprotectants under WL, probably because WL experiments are difficult to maintain; however, most available studies report positive effects (Table 2). Polyamines are among the most effective. In two maize genotypes waterlogged 2 cm above the soil surface, foliar 0.75 mM Spd improved Chl content, plant height and biomass; increased the activities of SOD, CAT, GR, APX and DHAR, levels of AsA, GSH and PAs; upregulated *ZmADC1* and *ZmSPDS2*; and suppressed ethylene biosynthesis, with stronger effects in the sensitive cultivar DH662 (Wang et al., 2022). Putrescine increased SOD and CAT activity in a dose-dependent manner in two citrus rootstocks waterlogged for 9 d (Mahdavian et al., 2020).

Regulating ethylene and other growth regulators is a second strategy. In wheat waterlogged for 5 d, the ethylene synthesis inhibitor amino-oxyacetic acid reduced MDA, H₂O₂, and EL, and lowered GSH and SOD, CAT, and POD activity relative to waterlogged plants (Rauf et al., 2021). Among several plant growth regulators tested in soybean waterlogged for 2 d, ethephon gave the best results, restoring shoot GSH content and GR activity, although roots responded oppositely, possibly because ROS levels were higher in shoots (Kim et al., 2018). Foliar SA reduced MDA, H₂O₂ and O₂^{•-} in two waxy maize lines waterlogged for 7 d, particularly in the WL-sensitive line, and differentially modulated SOD, POD and CAT (Wang et al., 2021); similar benefits of SA were reported in peony (Zhu et al., 2020).

Signaling molecules also mitigate WL-induced oxidative stress. Nitric oxide acts as both a signaling molecule and an antioxidant (Wani et al., 2021). When applied as sodium nitroprusside (SNP; 50, 500 and 2000 µmol L⁻¹) in irrigation

water, NO induced higher CAT, SOD and POD activity and higher AsA and phenol levels in a WL-resistant maize genotype after 21 h of stress (Jaiswal and Srivastava, 2018). In soybean, SNP and another NO donor, S-nitroso-L-cysteine, gave similar results, with genotype-dependent differences attributed to endogenous NO levels (Khan et al., 2019). Melatonin (100 µM) reduced EL and MDA in alfalfa waterlogged for 10 d (Zhang et al., 2019a), and H₂S supplied as 0.2 mM NaHS reduced EL, H₂O₂ and O₂^{•-} production in peach seedlings waterlogged for 72 h (Xiao et al., 2020).

Conclusion

Extreme temperature and WL cause oxidative stress that limits plant growth and productivity worldwide. While low levels of ROS act as signaling molecules, their uncontrolled accumulation damages proteins, lipids and nucleic acids. Enzymatic (SOD, CAT, APX, POD, and GR) and non-enzymatic (AsA, GSH, tocopherol, carotenoids, and flavonoids) antioxidants maintain the balance between ROS generation and detoxification. The studies reviewed here show that exogenous phytoprotectants such as PAs, amino acids, melatonin, fulvic acid, selenium, Pro, NO, SA, beneficial microbes and seaweed extracts can enhance antioxidant activity, reduce ROS accumulation, improve stress tolerance and sustain physiological functions under extreme temperature and WL. Their effects depend on crop type, stress intensity and exposure duration. Integrating phytoprotectant technologies with genetic improvement offers a promising pathway to cope with increasing climate variability. Future studies should focus on elucidating the underlying molecular mechanisms and on optimizing field-level application of phytoprotectants to mitigate oxidative stress, protect cellular structure and

Table 2. Effect of phytoprotectants on the regulation of reactive oxygen species under waterlogging.

Crop species	Duration of waterlogging	Dose of protectants	Regulatory effects	Reference
<i>Zea mays</i> (XD20, tolerant; DH662, sensitive)	WL, 2 cm above soil surface, ~5 d	Spd, 0.75 mM, foliar spray twice daily (07:00 and 19:00 h)	Improved Chl content, plant height and biomass; enhanced SOD, CAT, GR, APX and DHAR activity, AsA, GSH and PAs (Put, Spd and Spm); suppressed ethylene biosynthesis via downregulation of <i>ZmACS6</i> and <i>ZmACOC</i> ; stronger effects in DH662	Wang et al. (2022)
Carrizo citrange (<i>Citrus sinensis</i> Osb. × <i>Poncirus trifoliata</i> Raf.) and Volkameriana (<i>Citrus volkameriana</i>) rootstocks	WL, 9 d	Put, 1 and 2 mM, foliar spray	Dose-dependent increase in SOD and CAT activity in both rootstocks	Mahdavian et al. (2020)
<i>Z. mays</i> lines SY-MY13 (WL-resistant) and SYXT1 (WL-sensitive)	WL, 7 d	SA, 1 mM, foliar spray	Reduced MDA, H ₂ O ₂ and O ₂ ^{•−} content; enhanced SOD, POD and CAT activity	Wang et al. (2021)
<i>Paeonia suffruticosa</i> Andr. cvs. Fengdanbai and Mingxing	WL, up to 9 d	SA, 0.1, 0.5 and 1 mM, foliar spray	Reduced MDA content; increased SOD, POD and CAT activity; 0.5 mM SA most effective	Zhu et al. (2020)
<i>Prunus persica</i> (L.) Batsch	WL, 72 h	H ₂ S (0.2 mMNaHS), co-treatment	Reduced EL, H ₂ O ₂ content and O ₂ ^{•−} production rate; increased CAT, SOD and POD activity	Xiao et al. (2020)
<i>Glycine max</i> cv. Enrei	WL, 4 d	JA, 50 µM, co-treatment	Enhanced GST and MDHAR activity	Kamal and Setsuko (2016)
<i>Ficus carica</i> cv. Masui Dauphine	WL, 6 d	ALA, 5 mg L ^{−1} , pretreatment	Leaf O ₂ ^{•−} production 62.07% lower than in untreated waterlogged plants; reduced MDA content; enhanced SOD and POD activity	An et al. (2016)
<i>Z. mays</i> cvs. HUZM-265 (WL-resistant) and HUZM-55 (WL-susceptible)	WL, up to 21 h	NO as SNP, 50, 500 and 2000 µmol L ^{−1} , soil drench	Higher CAT activity at 18 h with 2000 µmol L ^{−1} SNP (resistant) and 50 µmol L ^{−1} SNP (susceptible); POD activity increased in both genotypes with 50 and 2000 µmol L ^{−1} SNP; at 21 h, SOD and APX activity increased in the resistant but decreased in the susceptible genotype; SNP restored AsA content	Jaiswal and Srivastava (2018)

maintain physiological functions under stress conditions.

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Author contribution

Dipanwita Datta: Writing – original draft, literature review; Samiul Alam: Writing – original draft, visualization; Faomida Sinthi: Writing – original draft, literature review; Kamrun Nahar¹: Literature review, writing – review and editing; Mirza Hasanuzzaman: Conceptualization, writing – review and editing.

Conflict of interest

The authors declare no conflict of interest.

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