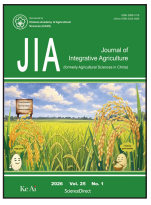
Journal of Integrative Agriculture 2026, 25(1): 1–15

Available online at ScienceDirect

Journal of Integrative Agriculture



REVIEW

Abiotic stress responses in crop plants: A multi-scale approach

Yanqing Wu[1], Jiao Liu[1], Lu Zhao[2], Hao Wu[1], Yiming Zhu[1], Irshad Ahmad[1, 2#], Guisheng Zhou[1, 2#]

[1] *Joint International Research Laboratory of Agriculture and Agri-Product Safety, Ministry of Education/Institute of Agricultural Science and Technology Development, Yangzhou University, Yangzhou 225009, China*

[2] *College for Overseas Education, Yangzhou University, Yangzhou 225000, China*

Highlights

- Abiotic stresses reduce crop yield and quality.
- Plants adapt to abiotic stresses through morpho-physiological and molecular mechanisms.
- Water stress lowers amylose but boosts stress-related proteins in plants.

Abstract

Global population pressures have necessitated increased focus on protecting and developing resilient plant species that can maintain productivity despite environmental challenges. Environmental degradation, driven by climate change and anthropogenic activities, poses significant threats to global food security through various forms of physical stress. Major environmental constraints affecting agricultural yields worldwide include salinity, water scarcity, nutritional imbalances (encompassing mineral toxicity and deficiencies), and extreme temperatures. Crop yield is influenced by multiple abiotic factors, including agronomic conditions, climatic variables, and soil nutrient availability. Plants develop various survival mechanisms at molecular, cellular, and physiological levels in response to stress. Abiotic stress, whether occurring individually or in combination, significantly impacts crop growth and productivity. For instance, drought stress reduces leaf area, plant height, and overall crop development. Cold stress inhibits plant development and crop efficiency, leading to diminished productivity. Salinity stress not only induces water stress in plants but also negatively affects cytosolic metabolism, cell development, membrane function, and increases reactive oxygen species (ROS) production. Elevated CO_2 concentrations may enhance global precipitation patterns, potentially resulting in increased rainfall that can adversely affect crop development. Plants under excessive water stress exhibit reduced amylose content but increased crude protein levels. This affects both quality and quantity of crop production by inhibiting seed germination and causing growth impairment through combined effects of elevated osmotic potential and ion toxicity. Plants have evolved various escape-avoidance and tolerance mechanisms in response to abiotic stress, including physiological adaptations and integrated cellular or molecular responses. This review paper examines the impact of abiotic stress on morpho-physiological, biochemical, and molecular activities across various crops. Additionally, it analyzes crop interactions with abiotic stress regarding response and adaptation mechanisms, providing a fundamental framework for species selection and development of stress-tolerant varieties in the future.

Keywords: morpho-physiological, abiotic stress, biochemical, molecular, crop productivity, salinity, drought, temperature stress, heavy metal, pant toxicity

1. Introduction

Abiotic stress significantly impacts crop growth and yield (Wu *et al.* 2023). These environmental factors negatively affect various aspects of crops, including productivity, lifecycle, survival, health, and adaptability (Ahmad *et al.* 2023b). Abiotic stress encompasses any adverse environmental condition that inhibits proper plant growth. Plants are exposed to multiple environmental variations in nature. Their sessile growth habit makes it challenging to cope with abiotic factors, forcing dependence on internal mechanisms

Received 9 April 2024; Received in revised form 7 June 2024; Accepted 2 July 2024; Available online 11 September 2024
Yanqing Wu, E-mail: yqwu@yzu.edu.cn; #Correspondence Irshad Ahmad, E-mail: irshadgadoon737@yahoo.com; Guisheng Zhou, E-mail: gszhou@yzu.edu.cn

© 2026 CAAS. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/). Peer review under responsibility of Editorial Board of *Journal of Integrative Agriculture*.
doi: 10.1016/j.jia.2024.09.003

to withstand external environmental changes. Plants struggle to develop in fluctuating environments; abiotic stress can cause morphological damage due to severe or persistent unfavorable conditions. Currently, human activities have caused serious environmental degradation alongside climate change, threatening global food security through environmental physical stress. Major environmental constraints affecting agricultural yield worldwide include salt stress, water deficiency, nutritional imbalances (including mineral toxicity and deficiencies), and temperature extremes (Fahad *et al.* 2017).

Abiotic stresses, including heavy metals, drought, cold, salt, and heat, significantly impair crop growth and yield (Tuteja and Gill 2016). Plant exposure to various abiotic stresses disrupts plant metabolism and morpho-physiological mechanisms, resulting in reduced crop productivity (Ben Rejeb *et al.* 2014). Research indicates that drought-induced stress manifests at all plant growth stages, affecting plants from molecular to morphological levels (Fahad *et al.* 2017). Studies show that drought impacts three critical plant stages: the pre-anthesis phase, before flowering; the terminal phase, after flowering; and vegetative development (Shavrukov *et al.* 2017). These interrelated abiotic stresses cause morpho-physiological, biological, and molecular changes in plants, significantly impacting growth and yield (Naya *et al.* 2007). Temperature critically influences plant growth, development, and yield (Fahad *et al.* 2017). During drought stress, high temperatures disrupt water flow from xylem to adjacent elongating cells, inhibiting cell elongation. This stress reduces leaf area, plant height, and crop development through decreased cell elongation, impaired mitosis, and limited expansion (Browse and Xin 2001). Temperature decline significantly affects plant geographic distribution and survival. Cold stress diminishes plant development and crop efficiency, causing yield losses (Pearce 2001). It inhibits growth and productivity by dehydrating cells and tissues and causing cellular water crystallization. Low temperatures increase electrolyte leakage and water stress due to impaired hydro-active stomata closure, reduced membrane conductivity, and increased water viscosity (Farooq *et al.* 2009). Additionally, it reduces plant metabolism, increases oxidative stress, and dissipates energy through free radical release (Devasirvatham and Tan 2018). Cold stress damages plants by modifying membrane structure and initiating cellular damage processes, including plasmolysis, protoplasmic streaming, and electrolyte leakage (Ahmad *et al.* 2023a). Changes in respiration rate harm cellular metabolism, and depending on stress intensity, abnormal anaerobic respiration produces aberrant metabolites. This cellular damage and altered metabolism result in reduced plant development, irregular fruit ripening, internal discoloration (vascular browning), increased decay susceptibility, and potential plant mortality (Takahashi *et al.* 2013). Temperature fluctuations, both high and low, can intensify drought stress through increased water loss *via* transpiration or evaporation. Heat stress occurs when crops experience prolonged exposure to temperatures beyond their optimal development range. High temperatures accelerate sexual development, limiting photosynthetic contribution to fruit or seed production. Elevated soil temperatures may prevent plant emergence. Beyond affecting plant growth, development, and seed germination, high temperatures can induce permanent drought stress with potentially lethal consequences (Ashkavand *et al.* 2018).

Water is essential for life, and plants depend on it for nutrition and movement. A deficiency in water results in drought stress, which significantly reduces plant vitality (Akbari *et al.* 2007). Salinity represents a major abiotic stress factor contributing to water stress in plants. This condition impedes the ability of roots to uptake water from the soil, as high salinity causes decreased soil water potential. Salinity typically occurs in semi-arid and arid regions where plants experience year-round higher rates of transpiration and evaporation compared to precipitation volume. Primary soil salinity results from natural salt accumulation in the subsurface, while secondary soil salinity stems from human-induced conditions such as environmental contamination. Secondary soil salinity can develop from irrigation with saline water, excessive fertilizer application, or alterations in soil composition (Flora *et al.* 2008). Elevated salt concentrations can induce ionic toxicity and osmotic stress. Research indicates that under normal conditions, plant cells maintain higher osmotic stress levels compared to soil, utilizing this elevated osmotic pressure to extract water and essential nutrients from the soil and store them in root cells. However, during salt stress, the soil's osmotic pressure exceeds that of plant cells. This occurs due to soil salt content, which limits the plant's ability to absorb water and minerals (Ca^{2+} and K^{+}). Furthermore, the movement of Cl^{-} and Na^{+} ions within plant cells damages cell membranes and cytosolic metabolism. Salinity negatively impacts cytosolic metabolism, cell development, membrane function, and increases reactive oxygen species (ROS) generation, affecting crop production quality and quantity. These effects include inhibited seed germination, growth impairment, and developmental damage due to combined effects of increased osmotic potential and specific ion toxicity (Flora *et al.* 2008).

Heavy metals, classified as non-biodegradable inorganic chemicals, possess an atomic mass exceeding 20 and a density greater than 5 g cm^{-3}. These metals exhibit toxicity to cells and genes, potentially inducing gene mutations through their influence on and contamination of soil, drinking water, food chains, irrigation systems, and surrounding environments (Schutzendubel and Polle 2002). Essential micronutrients (Mg, Zn, Cu, Fe, Mo, Mn, and Ni) present in soil are necessary for proper plant growth. Non-essential elements (Hg, Cd, As, Ag, Cr, Co, Sb, Pb, and Se) found in soil are not required for plant growth (Hall 2002). Plants can absorb heavy metals through both above- and below-ground surfaces. While plants require trace amounts of these elements for metabolism, growth, and development, their concentration increases throughout the crop cycle. Excessive levels of these elements can inhibit or diminish plant growth. Heavy metals at toxic levels disrupt various metabolic processes, leading to abnormal plant function. For example, they can alter or disturb protein structure by forming bonds with sulfhydryl groups (Hossain *et al.* 2015), potentially affecting functional groups of crucial biological components (Bray 2000).

Plants develop various tolerance and escape-avoidance mechanisms in response to abiotic stress, incorporating both integrated cellular or molecular responses and physical adaptation (Xiong *et al.* 2002). Important crops including maize (*Zea mays* L.), tomatoes (*Solanum lycopersicum* L.), soybeans (*Glycine max* L.), cotton (*Gossypium hirsutum* L.) and rice (*Oryza sativa* L.), demonstrate limited environmental adaptation when facing abiotic stress (Wang *et al.* 2017; Lu *et al.* 2018; Verma *et al.* 2018). Plants have developed sophisticated strategies utilizing plant transcription factors to counter abiotic stress effects (Magwanga *et al.* 2018; Raza *et al.* 2023). Plant coping mechanisms integrate physiological, molecular, and biochemical systems for stress detection, signal transduction pathways, endogenous hormones, and gene identification to prevent or minimize cellular oxidative damage (Ahmad *et al.* 2023a; Wu *et al.* 2023). Abiotic stress resistance encompasses tolerance and escape-avoidance mechanisms. Osmotic modification, which facilitates active solute accumulation in the cytoplasm to maintain cellular water balance, can mitigate abiotic stress effects (Ben Rejeb *et al.* 2014). The plant tolerance mechanism relies on efficient and rapid perception of abiotic factors, beginning with the innate basal defense system. This system triggers various signaling cascades and expression of genes responsible for inducing abiotic stress tolerance (Meena *et al.* 2017).

Plants demonstrate specific defense mechanisms that vary according to the nature of abiotic stimuli they encounter. These mechanisms encompass molecular remodeling, differential gene expression, and the production or secretion of biochemical substances (Onaga and Wydra 2016). Abiotic environmental stressors activate various tolerance mechanisms in plants, primarily biochemical and molecular responses (Wani 2018). Plants develop cellular strategies, termed biochemical tolerance processes, to minimize the impact of abiotic stress. This adaptive strategy includes developing insulating layers or physical barriers, secreting organic compounds or secondary metabolites, restructuring membrane components, and implementing internal mechanisms that sequester toxic compounds such as Al^{3+} into vacuoles or enhance antioxidant capacity (Bechtold and Field 2018).

The molecular mechanism of tolerance relies on genetic defense systems that plants develop against abiotic stress. Genetic mechanisms express multiple tolerance genes that encode transcriptional regulation and protein synthesis, supporting stress maintenance and reduction. Various transcription factors coordinate or enhance specific genes, thereby initiating distinct signaling pathways and promoting the development of stress-mitigating agents that regulate or reduce abiotic stress impacts (Cramer *et al.* 2011). Multiple abiotic stresses affect crops, with global warming and variable environmental conditions representing significant worldwide concerns. Crop productivity is affected by abiotic stresses including temperature extremes (both cold and heat), water availability fluctuations (scarcity and excess), and mineral or metal variations (excess metal (toxicity) or metal deficiency). Plants employ various mechanisms, including morpho-physiological, biochemical, and molecular processes, to manage abiotic stress effects. This review aims to address these adverse effects by examining these morpho-physiological and molecular processes in plants under abiotic stress.

2. Abiotic stress effects on crop

Abiotic factors reduce crop productivity through unavoidable environmental conditions. The effects of abiotic factors such as drought, salinity, cold, heat, and metal stress are challenging to quantify precisely. Based on plant dynamics and complexity, responses to abiotic stress can be categorized as elastic (reversible) or plastic (irreversible) (Farooq *et al.* 2009) (Fig. 1).

2.1. Drought stress

Water scarcity results in diminished plant growth and yield (Fig. 2). Plants respond to drought stress by closing stomata to preserve water, which consequently restricts CO_2 uptake and photosynthesis. Drought effects manifest across all phenological developmental stages, from morphological to molecular levels, primarily affecting yield. Drought conditions disrupt numerous physiological mechanisms in plants (Cattivelli *et al.* 2008). While productivity reduction depends on severity and duration, drought stress post-anthesis particularly impacts plant productivity regardless of these factors (Samarah 2005). Drought stress inhibits flower production and grain filling, affecting grain quantity and quality. While micro and macronutrients including nitrogen (N), potassium (K), and phosphorous (P) are vital for plant growth, drought stress substantially decreases P and increases N, with inconclusive effects on K (Farooq *et al.* 2009). Limited water availability impedes nutrient accessibility in the root zone, absorption at root hairs, and transport through xylem and phloem vessels, thus disrupting cellular nutrient metabolism (Ahmad *et al.* 2023c). Water facilitates mineral and nutrient transport, but reduced water availability decreases transpiration rates, leading to diminished nutrient uptake and utilization. Drought stress affects photosystems I and II and photosynthetic pigments including chlorophyll *a*, *b* and carotenoids (Yadav *et al.* 2020). It also impacts ribulose phosphatase, a Calvin cycle enzyme, resulting in decreased starch synthesis. Dehydration reduces cell size, increasing cellular content concentration. This process enhances protein–protein interaction aggregation and denaturation. Additionally, elevated solute concentrations may become toxic, adversely affecting enzyme function, including photosynthetic apparatus components, and increasing cytoplasmic viscosity (Parida and Das 2005).

2.2. Salinity stress

Plants face two primary challenges under salinity conditions: osmotic and ionic stresses (Ahmad I *et al.* 2022) (Fig. 3). Evidence indicates that salinity induces oxidative stress in plants. The adverse effects of salinity alter various plant physiological and metabolic processes. Common symptoms include increased leaf density and succulence, decreased leaf area, enhanced root and shoot necrosis, cell death, and reduced internode lengths. Prolonged exposure to salinity

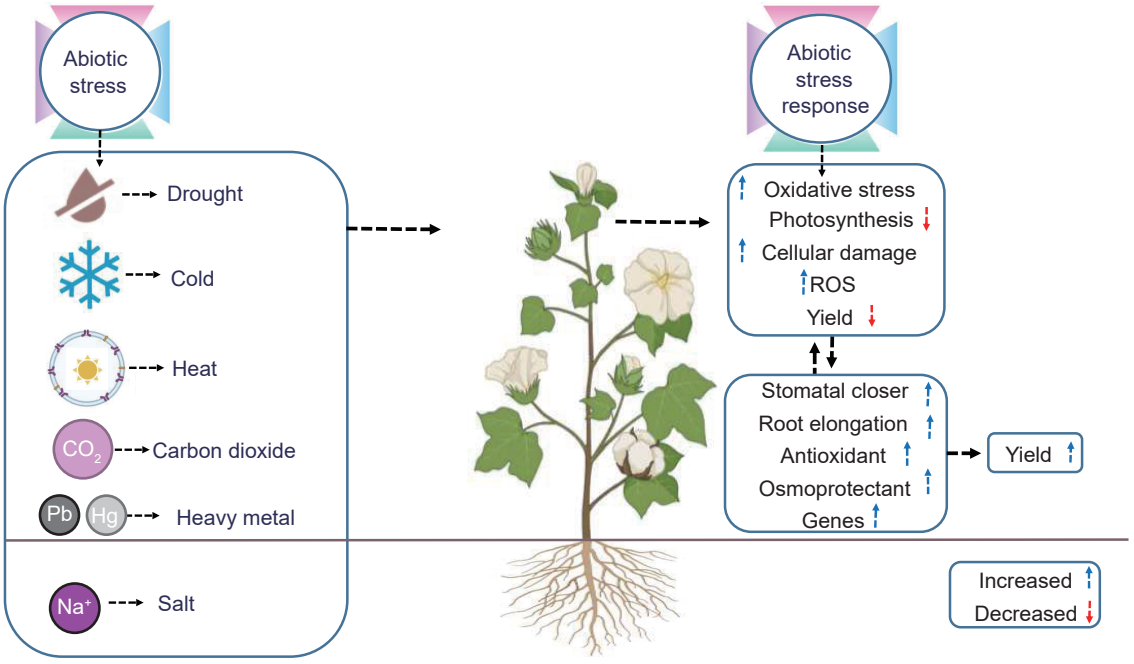


Fig. 1 Effects of abiotic stress on crops and their coping mechanisms. ROS, reactive oxygen species.

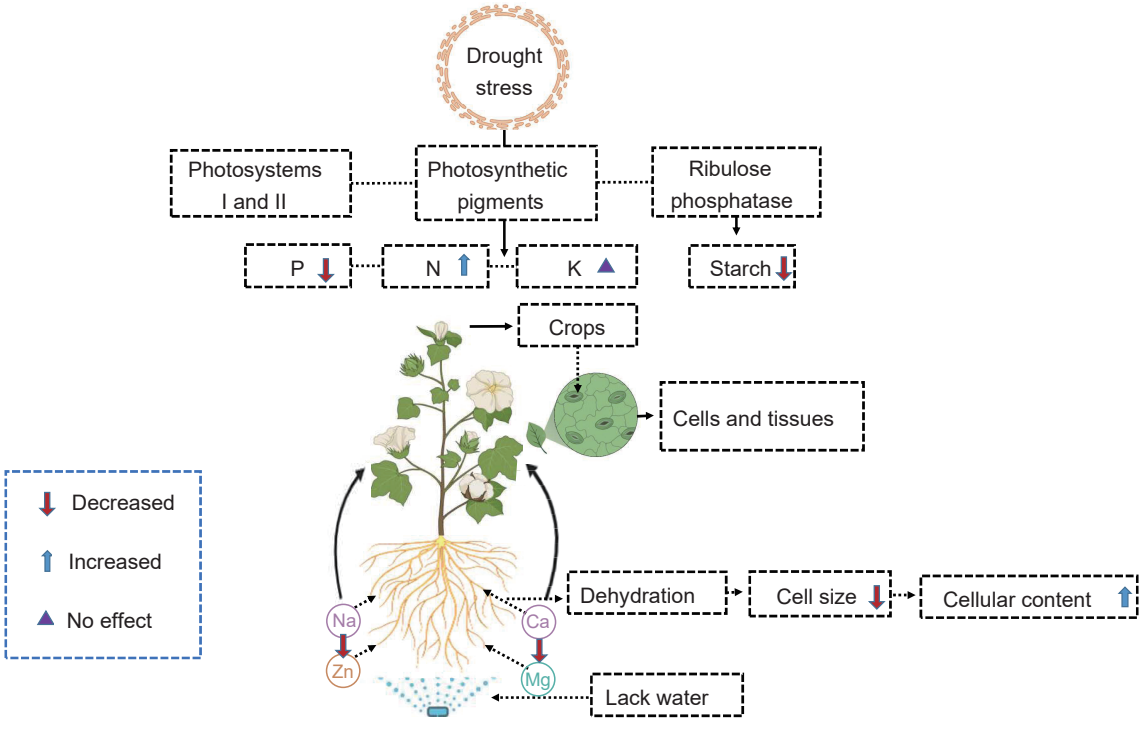


Fig. 2 Drought stress negatively impacts photosystem I and II, the photosynthesis system, and ribulose phosphatase, leading to decreased starch production. Furthermore, drought stress decreases phosphorous (P) levels while increasing nitrogen (N), with no impact on potash (K). In crops, reduced water availability in the root zone impairs nutrient uptake through root hairs, disrupting nutrient metabolism in cells and tissues. Cell dehydration causes cell shrinkage, consequently disturbing plant cellular content.

stress promotes cell senescence and restricts growth. While growth inhibition represents the primary damage leading to additional symptoms, severe salt shock may also trigger programmed cell death (Grattan and Grieve 1998). Salt stress stimulates abscisic acid production, inducing stomatal closure during transit to protect cells. The combination of oxidative

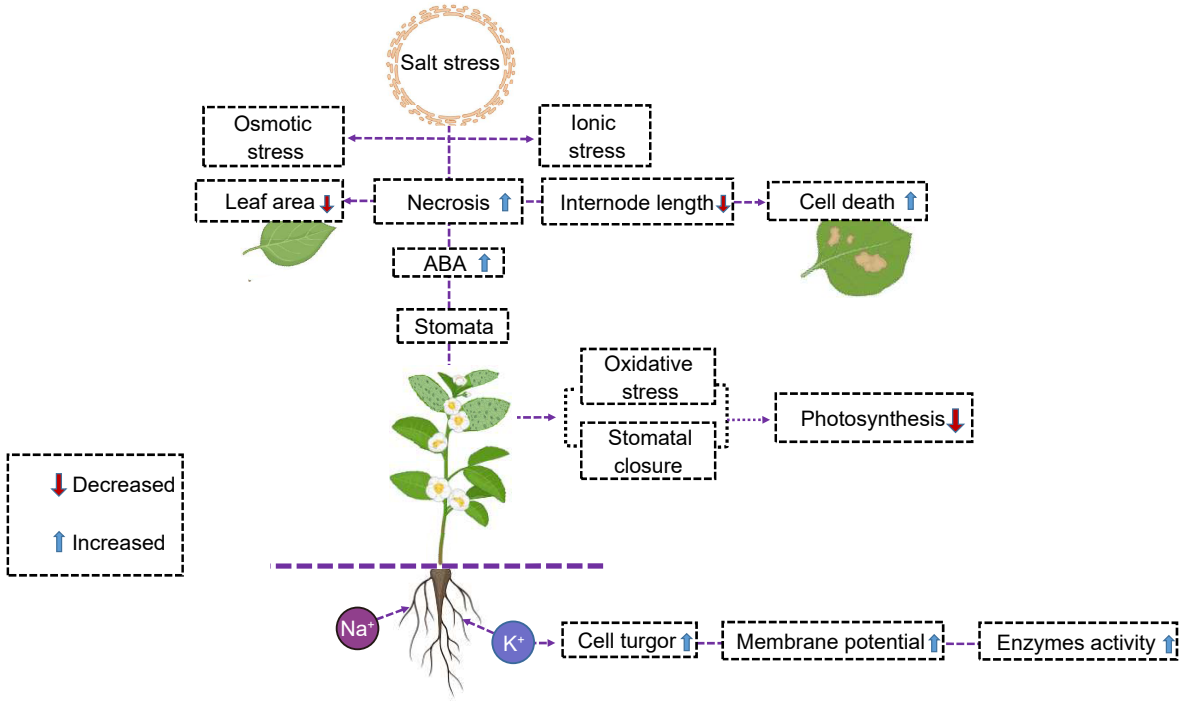


Fig. 3 Salt stress manifests primarily through osmotic and ionic stress mechanisms. This stress reduces leaf area, induces necrosis, decreases internode length, and in severe cases, leads to cell death. The stress triggers abscisic acid (ABA) production, which facilitates stomatal closure and cellular protection. The combination of oxidative stress and stomatal closure diminishes photosynthetic capacity. Osmotic stress inhibits cellular growth by disrupting ABA translocation, caused by elevated Na^+ concentrations in the root zone, while simultaneously impeding K^+ uptake. K^+ plays essential roles in maintaining cell turgor, membrane potential and enzymatic activity.

stress, stomatal closure, and photosynthetic suppression reduces photosynthetic efficiency. Osmotic stress can inhibit cell growth, either directly or indirectly, through its effects on abscisic acid metabolism and translocation. The high concentration of Na^+ near the root zone prevents K^+ uptake at the plant's root surface. Due to the biochemical similarity between K^+ and Na^+ ions, Na^+ strongly inhibits K^+ absorption by roots. Since K^+ serves as the predominant cellular cation and maintains cell turgor, membrane potential, and enzyme activity, potassium deficiency inevitably inhibits growth. When Na^+ enters the cytoplasm, many enzymes cease functioning or lose their operational capacity. This inhibition depends on K^+ concentration, with an elevated Na^+/K^+ ratio being most detrimental. Salinity-induced nutritional disturbances affect nutrient transport, availability, and partitioning, thereby limiting plant development. High salt levels can create nutrient imbalances or deficiencies as Na^+ and Cl^- compete with nutrients such as K^+, Ca^{2+}, and NO_3^-. The specific ion toxicity of Na^+ and Cl^-, combined with ionic imbalances in saline conditions, impacts plant growth through biophysical components and/or metabolic processes. Rice demonstrates greater salt tolerance during germination and vegetative stages compared to seedling and reproductive stages. High-yielding rice cultivars experienced approximately 12% yield reduction at salt levels exceeding 3 dS m^{-1}, increasing to approximately 50% at 6 dS m^{-1} (Reshma *et al.* 2021). According to Negrão *et al.* (2017), salt-stressed plants showed decreased leaf area, grains per panicle, leaf dry matter, tiller number, and pollen viability, alongside delayed seed germination, seed set, and sterile spikelets. Salt-exposed rice plants exhibit poor nutrient uptake, reduced water potential, and increased Cl^- and Na^+ uptake. Salinity stress also affects anthocyanin and proline levels, peroxidase activity, and concentrations of Na^+, Ca^{2+}, K^+, chlorophyll, and hydrogen peroxide (H_2O_2) (Ghomi *et al.* 2013). Salt stress significantly reduced amylose content in a salt-tolerant rice genotype but not in a semi-tolerant genotype, even under low electrical conductivity (EC 4 mS cm^{-1}) and high alkalinity (pH 9.5). Conversely, high electrical conductivity (EC 8 dS m^{-1}) and high alkalinity (pH 9.8) significantly reduced starch content in both genotypes, but not in the susceptible genotype (Barrero-Sicilia *et al.* 2017). Additionally, high salinity (EC 4 and 8 mS cm^{-1}) and high alkalinity (pH 9.8) altered gel consistency in the salt-susceptible genotype (Barrero-Sicilia *et al.* 2017).

2.3. Cold stress

Cold stress affects crops by causing surface lesions and reducing structural integrity, while also altering cell membrane composition and various metabolic processes (Flowers 2004) (Fig. 4). Environmental changes have led to increased severity, frequency, and duration of extreme temperatures. Temperature reduction disrupts plant physiological activities, with cold-sensitive plants exhibiting slower growth, reduced varietal options, and decreased yield potential. Plants respond to abiotic stresses through integrated metabolic,

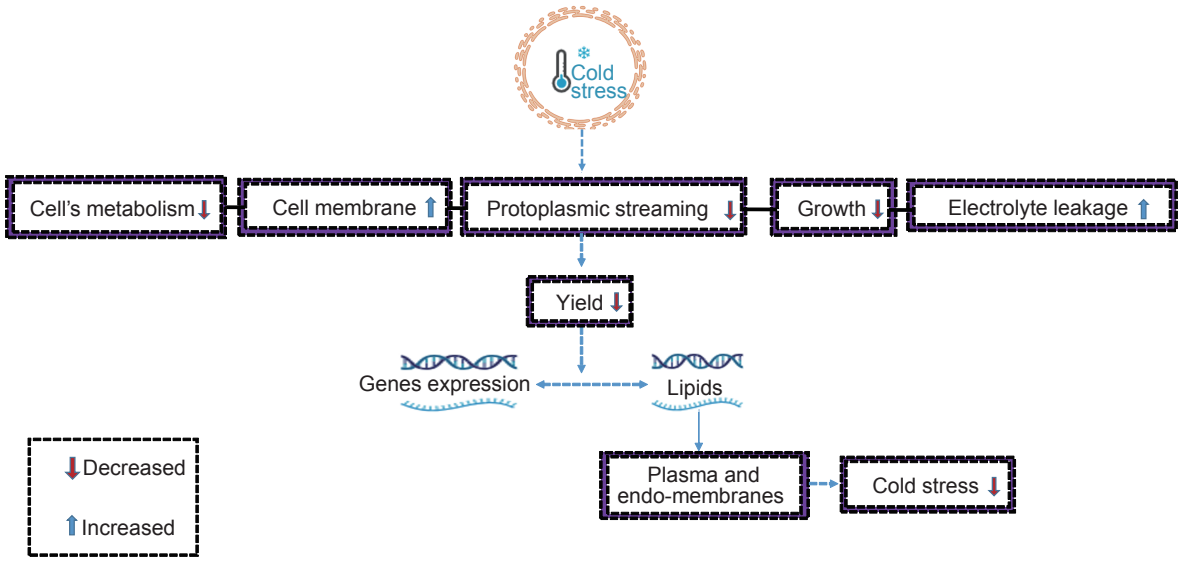


Fig. 4 Cold stress causes reduced plant growth, decreased protoplasmic streaming, increased electrolyte leakage and cell membrane damage, resulting in reduced yield. Gene expression and lipids, as key components of plasma and endo-membranes, are important for improving lipid structure and mitigating the negative effects of cold stress.

physiological and molecular adaptations, employing specific coping mechanisms. These mechanisms initially provide protective adaptations, followed by cold acclimatization that enhances cold stress tolerance (Nishida and Murata 1996). While transcription factors enhance stress-related gene expression, the transcriptional network extends beyond cold response pathways (Nishida and Murata 1996). Lipids, essential components of plasma and endo-membranes, serve crucial roles in membrane structure and cold stress mitigation (Chen and Thelen 2013). Cold stress reduces growth rate, affects cell membrane composition and structure, decreases protoplasmic streaming and electrolyte leakage, and modifies cellular metabolism (Takahashi *et al.* 2013). Additional cold stress responses include alterations in water and nutrient balance, modifications to protein and nucleic acid production, changes in enzyme binding and conformation, and photosynthetic disruptions, particularly regarding photosystem II down-regulation and damage (Miquel *et al.* 1993). Cells detect low temperatures through structural changes in protein and lipid membranes, maintaining metabolite equilibrium. The plasma membrane's fluid state provides structural and functional advantages for metabolic and physical processes. During temperature changes, the plasma membrane transitions from a fluid state at higher temperatures to a rigid gel state at lower temperatures (Janská *et al.* 2010). The physical alterations in membrane conformation at low temperatures primarily result from increased unsaturated lipid content, which enhances membrane stability and fluidity, enabling cellular mechanical adaptation to cold conditions (Wahid and Shabbir 2005).

2.4. Extreme or high temperature

High temperatures lead to modifications in biochemistry, physiology and morphology that disrupt plant growth and development (Moore *et al.* 2021). Research indicates that high temperatures represent one of the most damaging abiotic stresses, reducing grain biochemical components and productivity. High temperatures decrease overall biomass production by reducing photosynthesis and photorespiration (Smertenko *et al.* 1997).

High-temperature stress inhibits protein synthesis, causes severe protein damage, damages membranes, and inactivates essential enzymes. This stress significantly affects cell division processes (Dong *et al.* 2014). These adverse effects can severely impair plant growth and promote oxidative damage. Temperature increases become more detrimental when water supply is limited or suboptimal. Heat stress typically increases daytime transpiration rates, ultimately affecting various physiological processes in crops. Additionally, brief exposure to high temperatures during seed filling can result in accelerated filling, leading to reduced yield and quality. Post-anthesis elevated temperatures affect grain quality and appearance while reducing grain yield (Rang *et al.* 2011). Similarly, elevated temperatures reduce pollen viability and increase spikelet sterility, diminishing grain yield and quality (Ahmed *et al.* 2015). Extreme temperature stress during development reduces grain morphological characteristics, chalkiness (in rice), and biochemical characteristics, including amylose and protein content (Crafts-Brandner and Salvucci 2002). Elevated heat stress primarily affects the thylakoid stroma's light-dependent chemical processes, carbon metabolism, enhanced photosynthesis II thermo-tolerance adjustment for photon flux density, and photosynthesis II leaf temperature (Camejo *et al.* 2005). Photosynthesis II exhibits high temperature sensitivity and undergoes significant activity changes, including partial termination, under high heat stress (De Ronde *et al.* 2004). High temperatures severely damage the oxygen-evolving complex, potentially causing irregular electron flow to the photosynthesis II acceptor site (De Las Rivas and Barber

1997). Temperature-induced denaturation similarly affects proteins D1 and D2 (Vu *et al.* 2001). High heat stress substantially impacts the activity of vital enzymes including invertase, starch and sucrose synthesis, ADP-Glc PPase (adenosine di-pphosphate-glucose pyro-phosphorylase), and SPS (sucrose phosphate synthase) (Crafts-Brandner and Salvucci 2002). Higher temperatures inhibit starch production by decreasing sugar and starch metabolism, reducing grain filling and the quantity of filled grains per panicle (Hussain *et al.* 2017).

2.5. Carbon dioxide (CO_2) concentration

The reduced activation status of the CO_2 binding enzyme RuBisco decreases net photosynthesis in numerous plant species (Fig. 5). While RuBisco demonstrates improved catalytic activity at higher temperatures, its limited ability to bind carbon dioxide and oxygen restricts increases in net photosynthetic rate (Miquel *et al.* 1993). Despite these negative effects of high temperatures on photosynthesis, elevated atmospheric carbon dioxide concentrations are expected to increase the optimal temperature requirements for photosynthesis (Walter 2018). Research indicates that when CO_2 levels reach 685 parts per million by 2050, accompanied by a 3–6°C increase in global mean temperature above pre-industrial levels, environmental carbon-dioxide (eCO_2) becomes a significant factor affecting plant development (Fahad *et al.* 2017). Crop models suggest that eCO_2 levels may increase global precipitation, though significant regional variations in both space and time are possible. The irregular occurrence and intensity of rainfall may result in waterlogging and drought patches (Hussain *et al.* 2017). Multiple studies indicate that optimal levels of eCO_2 can mitigate drought stress effects.

2.6. Excessive water or submergence or flooding

Submerged rice experiences deterioration in both quality and quantity, particularly during maturity and seed production phases. Submergence negatively affects grain yield, shoot biomass, harvest index, and yield components, while significantly delaying flowering and maturity (Ferrero *et al.* 2020). The primary factors contributing to decreased grain yield under submergence conditions are reductions in grain weight, filling capacity, and number per panicle (Rascio and Navari-Izzo 2011). Submergence during the vegetative stage impacts critical grain quality parameters. Stressed rough rice exhibits higher percentages of hull, brown rice, and bran compared to non-stressed samples. Additional observations include increased chalky grains, hulling breakage, reduced amylose percentage, and elevated crude protein content. In submerged rice, researchers observed a negative correlation between starch accumulation and ADP-glucose pyrophosphorylase (AGPase) activity. AGPase catalyzes the initial committed step in starch production. In wheat and other plant species' leaves, ADP-glucose pyrophosphorylase activation occurs through posttranslational redox modification in response to light and sugars (Uzu *et al.* 2009).

2.7. Metal hazards

Heavy metal contamination from natural or anthropogenic sources presents a frequent and hazardous form of air

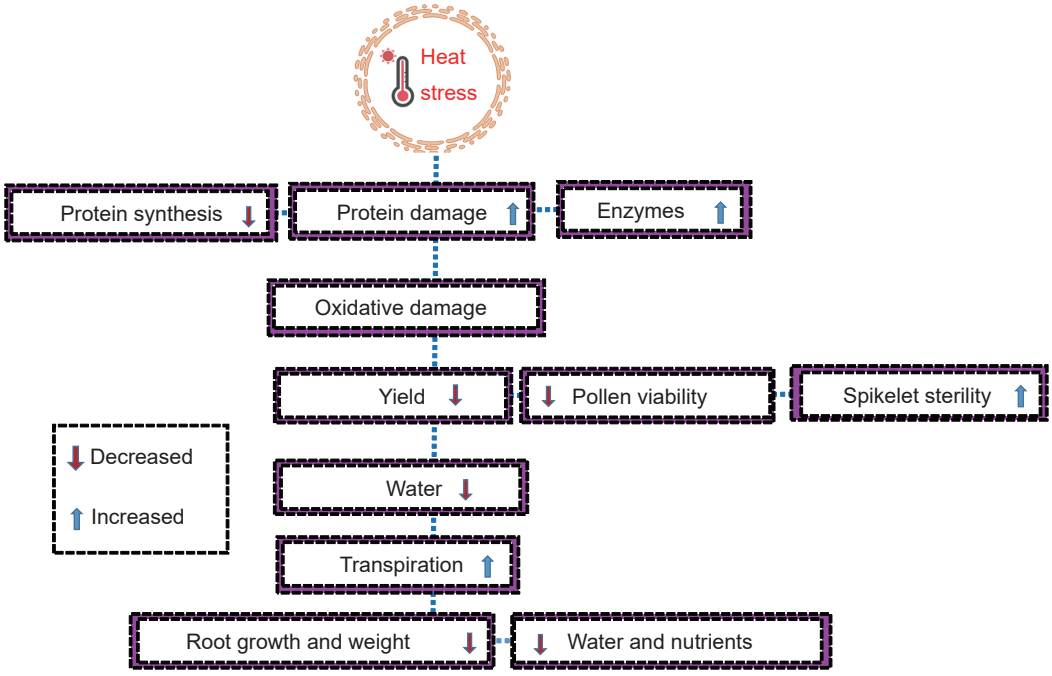


Fig. 5 Heat stress reduces protein synthesis, causes protein damage and affects enzyme activation. These changes in plants lead to oxidative damage, which subsequently reduces yield through decreased pollen viability and increased spikelet sterility. Furthermore, heat stress induces water loss due to elevated transpiration, which disrupts plant morpho-physiological activities such as root growth and weight, consequently reducing nutrient and water uptake.

pollution. Trace metals refer to various components present in soils at trace levels. Heavy metals comprise a broadly defined category of elements with atomic mass exceeding 20 (excluding alkali metals) and specific gravity greater than 5 (Pourrut *et al.* 2011). These metals exhibit varying bioavailability and solubility, manifesting in diverse forms within soil. Soil physicochemical properties influence heavy metal geochemical behavior, plant uptake patterns, and subsequent impacts on crop yield. Excessive heavy metal accumulation in plant tissue can adversely affect various morphological, physiological, and biochemical processes, either directly or indirectly, thereby significantly impacting crop productivity. Heavy metals negatively influence multiple physiological processes, including photosynthesis, seed germination, and the accumulation and remobilization of seed reserves during plant growth, resulting in reduced agricultural yield (Meers *et al.* 2009). Heavy metal toxicity diminishes plant productivity by disrupting redox balance, generating reactive oxygen species, and inducing oxidative stress through contaminated soil and water (Verbruggen *et al.* 2009). Metal accumulation occurs through root uptake, transfer to plant roots and shoots, and desorption from soil particles (Liao *et al.* 2006). Transpiration facilitates heavy metal transport through the xylem to aerial plant components (Maroco *et al.* 2000). After entering the central cylinder, metals migrate to upper plant regions *via* the vascular system's water stream, concentrating where water evaporation occurs (Chaves *et al.* 2003). Shoot tissues receive only a fraction of the heavy metals present in crops. Hyperaccumulator plants or those assisted by chelates may sequester up to 95% of metals through their roots.

3. Abiotic stress coping mechanisms in crops

Plants naturally develop defense mechanisms or survival strategies to manage adverse effects of abiotic stress factors. Plant resistance to abiotic stress manifests through multiple mechanisms, including tolerance, stress avoidance, and escape. In drought escape scenarios, plants develop efficient reproduction strategies before severe stress occurs. Plants maximize resource utilization while soil moisture remains adequate through combined short life cycles with rapid growth and gas exchange. This adaptation also involves avoiding unfavorable conditions through mechanisms such as stomatal closure, suppression of night-time germination, leaf abscission, and compact growth, specifically the reduction of plant parts (Wilson *et al.* 1980). Protective characteristics include enhanced root growth, nutrient redistribution from older leaves, reduced water loss, and increased photosynthetic and transpiration rates. These reversible physiological adaptations, achieved through decreased light absorption *via* leaf rolling, condensed canopy leaf areas, and stomatal closure, minimize morphological alterations in crops (Ingram and Bartels 1996). Tolerance represents concurrent physiological and biochemical modifications at cellular and molecular levels. Key adaptations include enhanced cell wall rigidity, reduced cell size, and osmotic adjustment (Alagoz *et al.* 2023). Sudden fluctuations in protein and mRNA levels indicate intolerance conditions. Crops undergo various morphological, physiological, biochemical, and molecular modifications to counter multiple abiotic stresses (Latef *et al.* 2019).

3.1. Morphological adaptation

In wheat crops, both single and combined stressors significantly decreased chlorophyll levels, leaf area index, relative water content, total dry matter, and grain yield. Conversely, stress conditions increased the content of carotenoid, proline, soluble sugars, and electrolyte leakage in wheat. Under water deficit conditions, the flowering stage exhibits greater sensitivity compared to the heading and kernel stages (Sherin *et al.* 2022).

Photosynthesis relies on chlorophyll pigments including chlorophyll *a*, *b* and carotenoids (Dehnavi *et al.* 2017; Latef *et al.* 2020). Various biotic and abiotic stressors adversely affect plant photosynthesis. Diminished photosynthetic pigments may result from reduced leaf surface area, which is essential for photosynthesis and light absorption (Ahmed *et al.* 2013). The chlorophyll pigment content in plants helps neutralize singlet oxygen radicals and indicates resilience to different types of abiotic stress (Liang *et al.* 2013). Tiryaki (2016) demonstrated that plants under combined salinity and drought stress show significant decreases in chlorophyll pigments, stomatal density, and transpiration rate.

Plants accumulate osmolytes to protect their internal processes from environmental changes, utilizing osmotic control to manage abiotic stresses (Dehnavi *et al.* 2017). Most crops synthesize low-molecular-weight organic solutes such as proline, cyclic polyols (inositol and derivatives of mono and di methylated inositol), glutamate, betaine (alanine or glycine), and linear polyols (mannitol, glycerol, or sorbitol) to counter salinity stress (Kumar and Sharma 2020). Proline and soluble sugars facilitate free radical elimination from cells and mitigate stress impacts on physiological processes by increasing cellular osmotic concentration (Seo *et al.* 2020). Wheat leaves demonstrated increased total soluble sugars and proline under salt and drought stress conditions (Shelden *et al.* 2013). Research indicates that extended root growth enhances plant resistance to drought and salinity stressors (Dos Santos *et al.* 2007). Salinity stress reduces fresh and dry root weight and restricts overall root growth in barley genotypes (Taleisnik *et al.* 2009). Dry soils show increased root biomass compared to regularly watered soils (Chamekh *et al.* 2014). Leaves, the primary photosynthetic organs, determine radiation interception. Restricted leaf growth represents one of the earliest observable effects of salt stress (Morales *et al.* 1998). Durum wheat genotypes exhibit decreased leaf area under salinity stress (Zheng *et al.* 2008). High salt concentrations significantly reduce both leaf area index (LAI) (El-Hendawy *et al.* 2005) and net assimilation rate (NAR) (Zaman *et al.* 2016). During tillering, wheat demonstrates correlation between initial LAI increase and increased leaf number and photosynthetic area. Leaf aging from stem base upward explains post-peak LAI decline. Premature leaf aging may cause NAR decrease. Reduced LAI and NAR potentially cause crop growth rate

(CGR) decline under water stress. Decreased CGR leads to lower dry matter accumulation and relative growth rate (RGR) during water deficit (Maiti and Satya 2014). Beena *et al.* (2018) reported significant NAR decrease, while other studies showed notable LAI reductions under drought stress (Hirabayashi *et al.* 2015).

Under extreme conditions, roots expand throughout the soil to access surrounding water and obtain sufficient moisture for survival. Root biomass increases when abiotic stress conditions promote root elongation and enhanced water absorption capacity. Plants with adequate translocation and transpiration mechanisms develop longer shoots compared to water-deficit plants struggling with nutritional and water deficiencies. The wheat shoot's tillers and internal mass influence its dry weight. Irrigated plants maintain tissue water content due to sufficient fresh water availability, while water-stressed plants experience reduced internal mass.

Morphological adaptations include genes that influence panicle coverage by foliage to maintain lower spikelet temperatures and higher spikelet fertility (Maroco *et al.* 2000). Plants that flower early in the morning can avoid elevated temperatures later in the day (Yadav and Sharma 2016). Abiotic stress induces morphological changes including biomass reduction, yield decrease, prolonged flowering period, reduced pollen viability, and altered photosynthetic capacity. These morphological modifications encompass anatomical changes such as thickened cell walls, increased chloroplast exposure to intercellular spaces, expanded mesophyll cell surface area, and distributed stomatal arrangement across leaf surfaces.

3.2. Physiological adaptation

Plants exhibit physiological adaptations to cope with abiotic stressors at cellular, molecular, and whole-plant levels. Relative turgidity represents the ratio between a leaf's actual water content at full turgor and its maximum water-holding capacity. Relative water content incorporates low water potential as a valuable plant water status indicator, along with osmotic adjustment's impact on maintaining cell hydration. Low water potential serves as an additional indicator of plant water status within relative water content, considering osmotic adjustment's role in cell hydration maintenance. Transpiration rate and water content are critical factors in leaf development. Plants undergo rapid transpiration as water moves from roots to leaves. This process leads to decreased water potential in drought-stressed plants and increased leaf water content in irrigated plants, a response unlikely in water-deficient plants (Cattivelli *et al.* 2008). This phenomenon reflects the actual damage experienced by stressed plants. Relative stress damage provides a metric for quantifying plant injury under stress conditions. Under stress, plants initiate environmental tolerance mechanisms and activate specific resistance genes. Abiotic stress tolerance appears to result from integrated physiological and biochemical changes at molecular and cellular levels, including osmotic adjustment, cell wall reinforcement, or cell size reduction. Stress tolerance manifests through rapid modifications in mRNA and protein levels (Tangpremsri *et al.* 1995).

Water use efficiency becomes crucial for crop productivity under limited water conditions. Agronomically, it represents the ratio of total dry matter (DM) harvested to water consumed. In essence, water use efficiency measures the relationship between transpired water and fixed carbon rates, or between agricultural production and water utilization. It is quantified through biomass produced per unit of transpiration. Achieving higher crop yields requires enhanced biomass production from limited water resources under stress conditions. During water deficits, plants may experience concurrent salinity and drought stress, necessitating appropriate water management strategies (El Hafid *et al.* 1998).

Plants develop various mechanisms to endure drought stress (Ahmad I *et al.* 2022). Furthermore, water-stressed crops exhibit stomatal closure, reducing CO_2 availability to leaves and increasing electron availability for active oxygen species formation (Turner *et al.* 2001). Environmental conditions that enhance transpiration elevate leaf sap pH, promote abscisic acid accumulation, and reduce stomatal activity (Bota *et al.* 2004). Severe drought conditions impair photosynthesis through decreased Rubisco activity (Bota *et al.* 2004). Evidence indicates that chloroplast CO_2 availability and photosystem II modifications during drought conditions regulate photosynthetic electron transport chain activity.

Osmotic adjustment (OA), characterized by increased intercellular solute concentration in response to water stress, maintains turgor at reduced water potential. Despite genotypic variations, researchers recognize osmotic adjustment as a fundamental mechanism for plant drought adaptation, enhancing tissue metabolic activity and regeneration capacity. Osmotic adjustment has been documented in drought-tolerant crops including wheat, sorghum, and oilseed brassicas. High ionic concentrations can significantly inhibit cytosolic enzymes in plant cells (Singh *et al.* 2017). During osmotic adjustment, vacuoles appear to restrict ion accumulation, maintaining separation between ions and the cytoplasm and subcellular organelles (Yadav *et al.* 2019). This ion compartmentalization necessitates the accumulation of alternative solutes, such as sugar alcohols and proline, in the cytoplasm to maintain cellular water potential equilibrium (Shaheen *et al.* 2016).

In wheat, plants naturally respond to water deficit by wilting, reducing leaf area, and leaf abscission to minimize water loss through transpiration. Significant water deficit inhibits plant cell elongation by impeding water movement from the xylem to elongating cells. During drought conditions, reduced cell elongation, expansion, and mitosis result in decreased plant height, leaf area, and crop development. Water conservation disrupts plant metabolism, induces stomatal closure, and compromises cell structure (Jagadish *et al.* 2007).

Extreme temperature stress disrupts cellular homeostasis in corn plants, inhibiting growth and development, potentially leading to mortality. High temperatures affect various stages of maize development differently. In soybeans, drought stress impacts germination rate and seedling vigor. Root length increases during water scarcity, while hypocotyl length, germination, and root and stem biomass decrease. Water deficiency negatively affects cell division and differentiation

processes essential for growth. Drought reduces turgor pressure, resulting in decreased cell elongation (Mukamuhirwa *et al.* 2019). Drought and high temperatures can severely impact plant development, causing reduced photosynthesis, diminished pollen production, irreversible growth damage, altered peduncle elongation, fewer panicles per plant, impaired pollen grain development, and increased spikelet sterility (Yang *et al.* 2019). Low temperatures delay heading, decrease spikelet fertility, inhibit seedling growth, reduce panicle development, cause poor panicle exertion, and diminish grain quality. Temperature and water stress affect both grain production and development while altering rice quality and chemical composition (Ahmad H *et al.* 2022).

Rice grain chalkiness increases under drought stress during the grain-filling period (Nithya *et al.* 2021). Research has shown that imposing drought stress for 30 days from anthesis onset resulted in decreased harvest index and grain yield across 25 rice genotypes, along with reduced grain test weight and pollen fertility in most genotypes (Cal *et al.* 2019). While leaf rolling is considered a protective response to drought stress, its occurrence correlates more strongly with morphological characteristics than water deficiency (Prince *et al.* 2015). Water shortage did not affect transpiration; however, certain genotypes such as Dangar exhibited increased leaf rolling (Rejeth *et al.* 2020). Drought stress affects root system architecture and influences genotype-dependent yield (Kumar *et al.* 2016). Plants have developed various adaptive responses to drought stress, including reduced leaf size, osmotic adjustment, decreased shoot water loss through enhanced cuticle deposition, and deeper root systems, which primarily maintain high internal water status (Sinha *et al.* 2022). Root architecture, water uptake, and osmotic adjustment have been identified as critical traits for drought tolerance screening.

An enhanced membrane stability index (MSI) reduces ROS damage to cell membranes, representing one of the physiological mechanisms enabling rice to tolerate heat stress (Xiong *et al.* 2014). Enhanced pollen viability ensures increased fertilization success, maintaining higher photosynthetic rates to offset yield losses from excessive transpiration under heat stress (Irato and Santovito 2021). Increased transpiration rates facilitate transpirational cooling to prevent ROS accumulation (Farooq *et al.* 2009). Physiological adaptations protect essential biological substances required for cellular homeostasis and membrane integrity. Heat shock proteins (HSPs) play a crucial role in cellular tolerance by maintaining protein tertiary structure. Additionally, both enzymatic and non-enzymatic antioxidants, including carotenoids, phenolic compounds, ascorbic acid, glutathione peroxidase (GPX), peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD), are essential for mitigating ROS effects (Krasensky and Jonak 2012).

3.3. Biochemical adaptation

Under abiotic stress, crops undergo various cellular, molecular and biochemical changes. Photosynthetic processes, adenosine triphosphate (ATP), and nicotinamide adenine dinucleotide (NAD) are essential for chlorophyll and carotenoid pigment production. Since chlorophyll cannot directly absorb sunlight, it must acquire it from carotenoid, an auxiliary pigment. Photosystems I and II utilize the light's energy to generate NADPH and ATP, two forms of chemical energy used by plants. Research indicates that plants utilize fixed CO_2 and photosystem products to synthesize glucose. Consequently, wheat with higher carotenoid content in its chloroplasts likely synthesizes more chlorophyll and absorbs more sunlight (Ashraf and Foolad 2007). Additionally, starch plays a vital role in plant adaptation to abiotic stress, including high temperatures, salt and drought. Under severe conditions that inhibit photosynthesis, plants typically utilize starch as an energy source. Plants can mitigate stress impacts by releasing appropriate solutes, derived sugars, osmoprotectants, and other metabolites to promote plant development (Panda and Sarkar 2014).

Arginine and proline are essential amino acids for regulating osmotic pressure under abiotic stress. Proline, functioning as an osmoprotectant, can enhance cell division while inhibiting it when present in excess. This proline accumulation pattern results from the expression of the pyrroline-5-carboxylate synthase gene. Additional evidence supporting proline's protective role comes from transgenic crops, where proline overproduction enhances tolerance to osmotic stress. Multiple amino acids contribute to osmotic stress response. Studies demonstrate that arginine effectively enhances stress tolerance in leaves. Under hyperosmotic stress, the enzyme associated with arginine production becomes activated. Moreover, under osmotic stress, sunflower and wheat plants demonstrate increased expression of asparagine synthase genes. Glutamate synthase overexpression in rice enhances its osmotic stress tolerance. These observations suggest that alterations in osmotic pressure-induced amino acid levels may result from modified gene expression encoding metabolic enzymes (Ahmad H *et al.* 2022). Additionally, survival rates under submerged conditions correlated positively with higher accumulation of starch and non-structural carbohydrates (Luo and Tang 2023).

In cotton, exogenous hormones, particularly mepiquate chloride (MC) and melatonin (MT), have been identified as the most effective abiotic stress signaling regulators (Wang *et al.* 2020; Song *et al.* 2023). Research demonstrates that MC enhances cotton production by reducing leaf area, plant height, and shoot and fruit branch length through decreased gibberellin (GA) production (Wu *et al.* 2023). Cotton plants treated with MC exhibited enhanced leaf weights, increased leaf thickness, elevated chlorophyll content, and improved net photosynthetic activity (Meng *et al.* 2023). It reduced ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO), modified the source–sink relationship, enhanced stomatal conductivity, and increased photoassimilate production in leaves (Kołodziejczyk *et al.* 2021). During middle and late leaf development stages, it increases active cytokinin (CK) levels, reduces GA synthesis, delays abscisic acid and ethylene peak times, and postpones leaf senescence onset. Studies indicate that MC application extends the functional period of cotton leaves (Khan *et al.* 2023). Salicylic acid (SA) and jasmonic acid (JA) improve plant tolerance to drought,

salinity and heat stresses. Previous research indicates that MT possesses strong antioxidant properties and can enhance crop resilience to abiotic stress through signal modulation (Zhang *et al.* 2021).

In plants, MT plays crucial roles in fruit ripening, photosynthetic activity, root and flower growth, leaf senescence, and mitigation of stress-induced oxidative damage (Posmyk 2016). MT enhances CAT, SOD, glutathione peroxidase (GSH-PX), glutathione reductase (GSSG-R), and ascorbate peroxidase (APX), enabling cotton to tolerate cold conditions through free radical scavenging (Li *et al.* 2018a). MT metabolites are distinct from most antioxidant enzymes in their ability to scavenge excess ROS and reactive nitrogen species (RNS) (Li *et al.* 2018b). MT enhances antioxidant activity during cold stress by optimizing redox state and gene expression (Qari *et al.* 2022). Additionally, MT improves cold resistance by enhancing antioxidant activity, starch degradation, and electron transport (Li *et al.* 2016). Studies have revealed multiple MT functions that contribute to stress tolerance across various crops (Wang *et al.* 2013). For example, during cadmium stress (Cd), MT treatment significantly reduced electrolyte leakage in tomatoes, while showing minimal effects under normal conditions (Wei *et al.* 2015). Appropriate MT levels enhance stress tolerance, total protein content, and cell fluid concentration in kiwifruit leaves, while promoting protein accumulation in *Malus hupehensis* (Galau *et al.* 1987). Under salt stress conditions, exogenous MT enhances soybean growth and protein content (Diamant *et al.* 2001).

3.4. Molecular adaptation

Late embryogenesis abundant (LEA) proteins, a class of high molecular weight proteins, are widely distributed during early embryogenesis and accumulate in response to water stress during seed dehydration. Multiple classes of LEA proteins have been documented. Among these groups, group 3 proteins are thought to assist in concentrated ion sequestration during cell dehydration. Group 1 LEA proteins demonstrate enhanced water-binding capacity, while group 5 LEA proteins are believed to regulate ions during water loss (Vierling 1991). Additionally, various detoxifying genes support defense against abiotic stress. Plants achieve stress protection through ROS scavenging and specific solute accumulation. This mechanism preserves protein structure and function. Studies indicate that genes activating ascorbate peroxidase, ascorbate peroxidase, and glutathione reductase influence multiple abiotic stressors (Piveta *et al.* 2020). A well-regulated biological response to heat or other abiotic stress involves increased transcription of specific gene groups across species. Heat shock transcription factor (HSF) operates as a monomeric, non-DNA binding form in unstressed cells. Under stress conditions, it forms a trimeric complex that binds heat shock gene promoters. The activation of genes encoding HSPs represents one of the most prominent responses in organisms exposed to elevated molecular temperatures (El-Esawi and Alayafi 2019).

Rice demonstrates differential overexpression of HSPs and heat shock factors (HSFs); HSF2a shows upregulation under heat stress, HSF7A exhibits upregulation during drought stress, and HSP74.8, HSP80.2, and HSP24.1 display upregulation under combined stress conditions (Radha *et al.* 2023). Furthermore, the expression of eight genes conferring abiotic stress tolerance (*OsRD29A*, *OsSNAC1*, *OsSNAC2*, *OsLEA3*, *OsDREB2A*, *OsDREB2B*, *OsRAB16A*, and *OsRAB16C*) and four genes encoding ROS-scavenging enzymes (OsSOD-Cu/Zn, OsCATB, OsCATA, and OsAPX2) demonstrates significant upregulation in transformed rice lines compared to wild-type expression (Juven-Gershon *et al.* 2008). Rice grain production increases with overexpression of the rice *Rab7* gene, enhancing resistance to drought and heat stress. Genomics and QTL-based approaches have facilitated the identification of genes and loci responsible for rice's abiotic stress resistance. These newly discovered molecular mechanisms enable rice to develop physiologically under suboptimal conditions while maintaining grain yield and reproductive development (Hu *et al.* 2006). Promoters function as specific regulatory sequences that bind transcription factors and RNA polymerase to initiate transcription (Shinozaki and Yamaguchi-Shinozaki 2007). The *trans*-regulatory elements involved in plant defense and stress-responsive gene regulation include zinc-finger families, basic-leucine zipper (bZIP), dehydration-responsive element-binding (DREB) or C-repeat binding factor (CBF), and MYB, which bind to the cis-element of corresponding gene promoters (Shinozaki and Yamaguchi-Shinozaki 2007).

Crops respond to abiotic stress through the activation of multiple genetic systems, including the ABA pathway, cold stress pathway, and SOS pathway. Under osmotic stress conditions, two pathways activate in plants: the ABA-independent pathways and the ABA-dependent pathways. ABA-response element (ABRE) binding protein and activated in plants. ABRE binding factors (AREB/ABFs) constitute transcription factors crucial to the ABA-dependent pathway. The transcription factors DREB2, a cis-element, and dehydration-response element/C-repeat (DRE/CRT) play essential roles in ABA-independent gene production during osmotic stress. AREB2/ABF4, ABF3, and AREB1/ABF2 expression increases progressively under drought and salt stress in vegetative tissues. Over-expression studies indicate these three ABRE binding protein and AREB/ABFs function as significant ABA regulatory signals during drought stress (Shi *et al.* 2000).

CBF/DREB1 homologs, identified across multiple species, bind to CRT/DRE *cis*-elements (A/GCCGAC) in the COR gene promoter region to regulate the expression of *COR* genes belonging to the ERF/AP2 (ethylene-responsive factor/APETALA2) transcription factor family. The CRT/DRE *cis*-acting elements regulate the expression of the *RD29A* gene, which contributes to abiotic stress response and tolerance (Gupta and Huang 2014).

SOS1, SOS2, and SOS3 are three essential enzymes involved in the SOS signaling pathway. The Na^+/H^+ anti-porter plasma membrane, which is crucial for regulating Na^+ efflux at the cellular level, is encoded by the SOS1 protein. Furthermore, its overexpression facilitates Na^+ long-distance transport from root to shoot and enhances plant salt tolerance (Tester and Davenport 2003). The *SOS2* gene, which

encodes serine/threonine kinase and contains a well-defined catalytic N-terminal domain and regulatory C-terminal region, is activated by Ca^{2+} signals that are elevated during salt stress. The SOS3 protein represents the third component in the SOS stress signaling system. It is a myristylated Ca^{2+} binding protein containing an N-terminus myristylation site. This site serves a critical function in salt tolerance by regulating vacuole activities, pH homeostasis, and membrane vesicle trafficking related to salinity tolerance. Consequently, when Na^+ concentration increases, there is a significant elevation in intracellular Ca^{2+} levels, which promotes its interaction with the SOS3 protein. Ca^{2+}, in conjunction with SOS proteins, regulates intracellular Na^+ homeostasis. Subsequently, the SOS3 protein interactions lead to the release of SOS2 protein's self-inhibition. The SOS2-SOS3 complex descends to the plasma membrane, where SOS1 responds. Phosphorylated SOS1 mitigates Na^+ toxicity by enhancing Na^+ efflux (El Mahi *et al.* 2019).

4. Conclusion

Environmental disturbances, whether arising from natural fluctuations or human interference, significantly impact crop productivity. The severity of abiotic stresses on crops ranges from subtle to catastrophic. Exposure to abiotic stress can disrupt plant metabolism, resulting in alterations to physiological processes, biochemical reactions, molecular modifications, and plant growth, ultimately affecting productivity. Crops have evolved various mechanisms to withstand the adverse effects of abiotic stresses, including enhanced relative stress injury, cell electrolyte leakage, decreased relative water content, elevated ROS production, reduced photosynthetic pigment, diminished root and shoot length, decreased yield, signal transduction pathways, endogenous hormones, and gene identification. Research demonstrates that crops employ multiple coping mechanisms integrating physiological, morphological, biochemical, and molecular modifications to mitigate the impacts of abiotic stresses.

Acknowledgements

The research was financially supported by the National Key R&D Program of China (2022YFE0113400), the Jiangsu Provincial Fund for Realizing Carbon Emission Peaking and Neutralization, China (BE2022305), the National Natural Science Fundation of China (32102411), and the Project funded by China Postdoctoral Science Foundation (2022M722698).

Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used ChatGPT 4.0 to assist in improving the clarity and readability of the language. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

References

Ahmad H, Zafar S A, Naeem M K, Shokat S, Inam S, Naveed S A, Xu J, Li Z, Ali G M, Khan M R. 2022. Impact of pre-anthesis drought stress on physiology, yield-related traits, and drought-responsive genes in green super rice. *Frontiers in Genetics*, **13**, 832542.

Ahmad I, Song X D, Ibrahim M E H, Jamal Y, Younas M U, Zhu G L, Zhou G S, Ali A Y A. 2023a. The role of melatonin in plant growth and metabolism, and its interplay with nitric oxide and auxin in plants under different types of abiotic stress. *Frontiers in Plant Science*, **14**, 1108507.

Ahmad I, Zhu G, Zhou G, Liu J, Younas M U, Zhu Y. 2023b. Melatonin role in plant growth and physiology under abiotic stress. *International Journal of Molecular Sciences*, **24**, 8759.

Ahmad I, Zhu G, Zhou G, Song X, Ibrahim M E H, Salih E G I, Hussain S, Younas M U. 2022. Pivotal role of phytohormones and their responsive genes in plant growth and their signaling and transduction pathway under salt stress in cotton. *International Journal of Molecular Sciences*, **23**, 7339.

Ahmad I, Zhu G, Zhou G, Younas M U, Suliman M E, Liu J, Zhu Y M, Gabralla E I S. 2023c. Integrated approaches for increasing plant yield under salt stress. *Frontiers in Plant Science*, **14**, 1215343.

Ahmed I M, Cao F, Zhang M, Chen X, Zhang G, Wu F. 2013. Difference in yield and physiological features in response to drought and salinity combined stress during anthesis in Tibetan wild and cultivated barleys. *PLoS ONE*, **8**, e77869.

Ahmed N, Tetlow I J, Nawaz S, Iqbal A, Mubin M, ul Rehman M S N, Butt A, Lightfoot D A, Maekawa M. 2015. Effect of high temperature on grain filling period, yield, amylose content and activity of starch biosynthesis enzymes in endosperm of basmati rice. *Journal of the Science of Food and Agriculture*, **95**, 2237–2243.

Akbari G, Sanavy S, Yousefzadeh S. 2007. Effect of auxin and salt stress (NaCl) on seed germination of wheat cultivars (*Triticum aestivum* L.). *Pakistan Journal of Biological Sciences*, **10**, 2557–2561.

Alagoz S M, Hadi H, Toorchi M, Pawłowski T A, Lajayer B A, Price G W, Farooq M, Astatkie T. 2023. Morpho-physiological responses and growth indices of triticale to drought and salt stresses. *Scientific Reports*, **13**, 8896.

Ashkavand P, Zarafshar M, Tabari M, Mirzaie J, Nikpour A, Bordbar S K, Struve D, Striker G G. 2018. Application of SiO_2 nanoparticles as pretreatment alleviates the impact of drought on the physiological performance of *Prunus mahaleb* (Rosaceae). *Boletín de la Sociedad Argentina de Botánica*, **53**, 1–10.

Ashraf M, Foolad M R. 2007. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany*, **59**, 206–216.

Barrero-Sicilia C, Silvestre S, Haslam R P, Michaelson L V. 2017. Lipid remodelling: Unravelling the response to cold stress in *Arabidopsis* and its extremophile relative *Eutrema salsugineum*. *Plant Science*, **263**, 194–200.

Bechtold U, Field B. 2018. *Molecular Mechanisms Controlling Plant Growth During Abiotic Stress*. Oxford University Press, UK. pp. 2753–2758.

Beena R, Vighneswaran V, Narayankutty M. 2018. Evaluation of rice genotypes for acquired thermo-tolerance using temperature induction response (TIR) technique. *Oryza — An International Journal on Rice*, **55**, 285–291.

Bota J, Medrano H, Flexas J. 2004. Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? *New Phytologist*, **162**, 671–681.

Bray E A, Bailey-Serres J, Weretilnyk E. 2000. Responses to abiotic stresses. *Biochemistry and Molecular Biology of Plants*. American Society of Plant Physiologists, Rockville, Maryland (MD), USA. pp. 1158–1203.

Browse J, Xin Z. 2001. Temperature sensing and cold acclimation. *Current Opinion in Plant Biology*, **4**, 241–246.

Cal A J, Sanciangco M, Rebolledo M C, Luquet D, Torres R O, McNally K L, Henry A. 2019. Leaf morphology, rather than plant water status, underlies genetic variation of rice leaf rolling under drought. *Plant, Cell & Environment*, **42**, 1532–1544.

Camejo D, Rodríguez P, Morales M A, Dell'Amico J M, Torrecillas A, Alarcón J J. 2005. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *Journal of Plant Physiology*, **162**, 281–289.

Cattivelli L, Rizza F, Badeck F W, Mazzucotelli E, Mastrangelo A M, Francia E, Marè C, Tondelli A, Stanca A M. 2008. Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. *Field Crops Research*, **105**, 1–14.

Chamekh Z, Ayed S, Sahli A, Ayadi S, Hammemi Z, Jallouli S, Trifa Y, Amara H, Mezghenni H, Hamrouni L. 2014. Effect of salt stress on the flag leaf area and yield components in twenty five durum wheat genotypes (*Triticum turgidum* ssp. durum). *Journal of New Sciences*, **50**, 3.

Chaves M M, Maroco J P, Pereira J S. 2003. Understanding plant responses to drought — From genes to the whole plant. *Functional Plant Biology*, **30**, 239–264.

Chen M, Thelen J J. 2013. Acyl-lipid *desaturase2* is required for chilling and freezing tolerance in *Arabidopsis*. *The Plant Cell*, **25**, 1430–1444.

Crafts-Brandner S J, Salvucci M E. 2002. Sensitivity of photosynthesis in a C_4 plant, maize, to heat stress. *Plant Physiology*, **129**, 1773–1780.

Cramer G R, Urano K, Delrot S, Pezzotti M, Shinozaki K. 2011. Effects of abiotic stress on plants: A systems biology perspective. *BMC Plant Biology*, **11**, 1–14.

Dehnavi M M, Zarei T, Khajeeyan R, Merajipoor M. 2017. Drought and salinity impacts on bread wheat in a hydroponic culture: A physiological comparison. *Journal of Plant Physiology and Breeding*, **7**, 61–74.

Devasirvatham V, Tan D K. 2018. Impact of high temperature and drought stresses on chickpea production. *Agronomy*, **8**, 145.

Diamant S, Eliahu N, Rosenthal D, Goloubinoff P. 2001. Chemical chaperones regulate molecular chaperones *in vitro* and in cells under combined salt and heat stresses. *Journal of Biological Chemistry*, **276**, 39586–39591.

Dong W, Chen J, Wang L, Tian Y, Zhang B, Lai Y, Meng Y, Qian C, Guo J. 2014. Impacts of nighttime post-anthesis warming on rice productivity and grain quality in East China. *The Crop Journal*, **2**, 63–69.

El-Esawi M A, Alayafi A A. 2019. Overexpression of rice *Rab7* gene improves drought and heat tolerance and increases grain yield in rice (*Oryza sativa* L.). *Genes*, **10**, 56.

Fahad S, Bajwa A A, Nazir U, Anjum S A, Farooq A, Zohaib A, Sadia S, Nasim W, Adkins S, Saud S. 2017. Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*, **8**, 1147.

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra S. 2009. Plant drought stress: Effects, mechanisms and management. *Sustainable Agriculture*, **29**, 153–188.

Ferrero D M, Piattoni C V, Diez M D A, Rojas B E, Hartman M D, Ballicora M A, Iglesias A A. 2020. Phosphorylation of ADP-glucose pyrophosphorylase during wheat seeds development. *Frontiers in Plant Science*, **11**, 1058.

Flora S, Mittal M, Mehta A. 2008. Heavy metal induced oxidative stress & its possible reversal by chelation therapy. *Indian Journal of Medical Research*, **128**, 501–523.

Flowers T. 2004. Improving crop salt tolerance. *Journal of Experimental Botany*, **55**, 307–319.

Galau G A, Bijaisoradat N, Hughes D W. 1987. Accumulation kinetics of cotton late embryogenesis-abundant mRNAs and storage protein mRNAs: Coordinate regulation during embryogenesis and the role of abscisic acid. *Developmental Biology*, **123**, 198–212.

Ghomi K, Rabiei B, Sabouri H, Sabouri A. 2013. Mapping QTLs for traits related to salinity tolerance at seedling stage of rice (*Oryza sativa* L.): An agrigenomics study of an Iranian rice population. *Omics*: *A Journal of Integrative Biology*, **17**, 242–251.

Grattan S, Grieve C. 1998. Salinity–mineral nutrient relations in horticultural crops. *Scientia Horticulturae*, **78**, 127–157.

Gupta B, Huang B. 2014. Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. *International Journal of Genomics*, **2014** , 701596.

El Hafid R, Smith D H, Karrou M, Samir K. 1998. Physiological responses of spring durum wheat cultivars to early-season drought in a Mediterranean environment. *Annals of Botany*, **81**, 363–370.

Hall J Á. 2002. Cellular mechanisms for heavy metal detoxification and tolerance. *Journal of Experimental Botany*, **53**, 1–11.

El-Hendawy S E, Hu Y, Schmidhalter U. 2005. Growth, ion content, gas exchange, and water relations of wheat genotypes differing in salt tolerances. *Australian Journal of Agricultural Research*, **56**, 123–134.

Hirabayashi H, Sasaki K, Kambe T, Gannaban R B, Miras M A, Mendioro M S, Simon E V, Lumanglas P D, Fujita D, Takemoto-Kuno Y. 2015. *qEMF3*, a novel QTL for the early-morning flowering trait from wild rice, *Oryza* officinalis, to mitigate heat stress damage at flowering in rice, *O. sativa*. *Journal of Experimental Botany*, **66**, 1227–1236.

Hossain Z, Mustafa G, Komatsu S. 2015. Plant responses to nanoparticle stress. *International Journal of Molecular Sciences*, **16**, 26644–26653.

Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L. 2006. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 12987–12992.

Hussain S, Zhang J H, Zhong C, Zhu L F, Cao X C, Yu S M, Bohr J A, Hu J J, Jin Q Y. 2017. Effects of salt stress on rice growth, development characteristics, and the regulating ways: A review. *Journal of Integrative Agriculture*, **16**, 2357–2374.

Ingram J, Bartels D. 1996. The molecular basis of dehydration tolerance in plants. *Annual Review of Plant Biology*, **47**, 377–403.

Irato P, Santovito G. 2021. Enzymatic and non-enzymatic molecules with antioxidant function. *Antioxidants* (Basel, Switzerland), **10**, 579.

Jagadish S K, Craufurd P Q, Wheeler T. 2007. High temperature stress and spikelet fertility in rice (*Oryza sativa* L.). *Journal of Experimental Botany*, **58**, 1627–1635.

Janská A, Maršík P, Zelenková S, Ovesná J. 2010. Cold stress and acclimation — What is important for metabolic adjustment? *Plant Biology*, **12**, 395–405.

Juven-Gershon T, Hsu J Y, Theisen J W, Kadonaga J T. 2008. The RNA polymerase II core promoter — The gateway to transcription. *Current Opinion in Cell Biology*, **20**, 253–259.

Khan T A, Saleem M, Fariduddin Q. 2023. Melatonin influences stomatal behavior, root morphology, cell viability, photosynthetic responses, fruit yield, and fruit quality of tomato plants exposed to salt stress. *Journal of Plant Growth Regulation*, **42**, 2408–2432.

Kołodziejczyk I, Kaźmierczak A, Posmyk M M. 2021. Melatonin application modifies antioxidant defense and induces endoreplication in maize seeds exposed to chilling stress. *International Journal of Molecular Sciences*, **22**, 8628.

Krasensky J, Jonak C. 2012. Drought, salt, and temperature stress-induced metabolic rearrangements and regulatory networks. *Journal of Experimental Botany*, **63**, 1593–1608.

Kumar N, Shankhdhar S C, Shankhdhar D. 2016. Impact of elevated temperature on antioxidant activity and membrane stability in different genotypes of rice (*Oryza sativa* L.). *Indian Journal of Plant Physiology*, **21**, 37–43.

Kumar P, Sharma P K. 2020. Soil salinity and food security in India. *Frontiers in Sustainable Food Systems*, **4**, 533781.

Latef A A H A, Alhmad M F A, Kordrostami M, Abo-Baker A B, Zakir A. 2020. Inoculation with *Azospirillum lipoferum* or *Azotobacter chroococcum* reinforces maize growth by improving physiological activities under saline conditions. *Journal of Plant Growth Regulation*, **39**, 1293–1306.

Latef A A H A, Mostofa M G, Rahman M M, Abdel-Farid I B, Tran L S P. 2019. Extracts from yeast and carrot roots enhance maize performance under seawater-induced salt stress by altering physio-biochemical characteristics of stressed plants. *Journal of Plant Growth Regulation*, **38**, 966–979.

Li M Q, Hasan M K, Li C X, Ahammed G J, Xia X J, Shi K, Zhou Y H, Reiter R J, Yu J Q, Xu M X. 2016. Melatonin mediates selenium-induced tolerance to cadmium stress in tomato plants. *Journal of Pineal Research*, **61**, 291–302.

Li X, Brestic M, Tan D X, Zivcak M, Zhu X, Liu S, Song F, Reiter R J, Liu F. 2018a. Melatonin alleviates low PS I-limited carbon assimilation under elevated CO_2 and enhances the cold tolerance of offspring in chlorophyll *b*-deficient mutant wheat. *Journal of Pineal Research*, **64**, e12453.

Li X, Wei J P, Scott E R, Liu J W, Guo S, Li Y, Zhang L, Han W Y. 2018b. Exogenous melatonin alleviates cold stress by promoting antioxidant defense and redox homeostasis in *Camellia sinensis* L. *Molecules*, **23**, 165.

Liang X, Zhang L, Natarajan S K, Becker D F. 2013. Proline mechanisms of stress survival. *Antioxidants & Redox Signaling*, **19**, 998–1011.

Liao Y, Chien S C, Wang M, Shen Y, Hung P, Das B. 2006. Effect of

transpiration on Pb uptake by lettuce and on water soluble low molecular weight organic acids in rhizosphere. *Chemosphere*, **65**, 343–351.
Lu P, Magwanga R O, Guo X, Kirungu J N, Lu H, Cai X, Zhou Z, Wei Y, Wang X, Zhang Z. 2018. Genome-wide analysis of multidrug and toxic compound extrusion (MATE) family in *Gossypium raimondii* and *Gossypium arboreum* and its expression analysis under salt, cadmium, and drought stress. *G3 — Genes*, *Genomes*, *Genetics*, **8**, 2483–2500.
Luo H, Tang F. 2023. Mepiquat chloride application combined with high plant population density promotes carbon remobilization in the roots of upland cotton. *Plant Physiology and Biochemistry*, **194**, 70–84.
Magwanga R O, Lu P, Kirungu J N, Lu H, Wang X, Cai X, Zhou Z, Zhang Z, Salih H, Wang K. 2018. Characterization of the late embryogenesis abundant (LEA) proteins family and their role in drought stress tolerance in upland cotton. *BMC Genetics*, **19**, 1–31.
El Mahi H, Pérez-Hormaeche J, De Luca A, Villalta I, Espartero J, Gámez-Arjona F, Fernández J L, Bundó M, Mendoza I, Mieulet D. 2019. A critical role of sodium flux *via* the plasma membrane Na^+/H^+ exchanger SOS1 in the salt tolerance of rice. *Plant Physiology*, **180**, 1046–1065.
Maiti R, Satya P. 2014. Research advances in major cereal crops for adaptation to abiotic stresses. *GM Crops & Food*, **5**, 259–279.
Maroco J P, Pereira J S, Chaves M M. 2000. Growth, photosynthesis and water-use efficiency of two C_4 Sahelian grasses subjected to water deficits. *Journal of Arid Environments*, **45**, 119–137.
Meena K K, Sorty A M, Bitla U M, Choudhary K, Gupta P, Pareek A, Singh D P, Prabha R, Sahu P K, Gupta V K. 2017. Abiotic stress responses and microbe-mediated mitigation in plants: The omics strategies. *Frontiers in Plant Science*, **8**, 172.
Meers E, Qadir M, De Caritat P, Tack F, Du Laing G, Zia M. 2009. EDTA-assisted Pb phytoextraction. *Chemosphere*, **74**, 1279–1291.
Meng L, Yu K, Wei Z, Li K, Dai J, Li F, Qi H, Sun L, Zhang L, Dong H. 2023. High dosage of mepiquat chloride delays defoliation of harvest aids in cotton. *Industrial Crops and Products*, **202**, 116998.
Miquel M, James Jr D, Dooner H, Browse J. 1993. *Arabidopsis* requires polyunsaturated lipids for low-temperature survival. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 6208–6212.
Moore C E, Meacham-Hensold K, Lemonnier P, Slattery R A, Benjamin C, Bernacchi C J, Lawson T, Cavanagh A P. 2021. The effect of increasing temperature on crop photosynthesis: From enzymes to ecosystems. *Journal of Experimental Botany*, **72**, 2822–2844.
Morales M, Sánchez-Blanco M, Olmos E, Torrecillas A, Alarcon J. 1998. Changes in the growth, leaf water relations and cell ultrastructure in *Argyranthemum coronopifolium* plants under saline conditions. *Journal of Plant Physiology*, **153**, 174–180.
Mukamuhirwa A, Persson Hovmalm H, Bolinsson H, Ortiz R, Nyamangyoku O, Johansson E. 2019. Concurrent drought and temperature stress in rice — A possible result of the predicted climate change: Effects on yield attributes, eating characteristics, and health promoting compounds. *International Journal of Environmental Research and Public Health*, **16**, 1043.
Naya L, Ladrera R, Ramos J, González E M, Arrese-Igor C, Minchin F R, Becana M. 2007. The response of carbon metabolism and antioxidant defenses of alfalfa nodules to drought stress and to the subsequent recovery of plants. *Plant Physiology*, **144**, 1104–1114.
Negrão S, Schmöckel S, Tester M. 2017. Evaluating physiological responses of plants to salinity stress. *Annals of Botany*, **119**, 1–11.
Nishida I, Murata N. 1996. Chilling sensitivity in plants and cyanobacteria: The crucial contribution of membrane lipids. *Annual Review of Plant Biology*, **47**, 541–568.
Nithya N, Beena R, Abida P, Sreekumar J, Stephen R, Jayalekshmi V, Manju R, Viji M. 2021. Genetic diversity and population structure analysis of bold type rice collection from Southern India. *Cereal Research Communications*, **49**, 311–328.
Onaga G, Wydra K. 2016. Advances in plant tolerance to abiotic stresses. *Plant Genomics*, **10**, 229–272.
Panda D, Sarkar R K. 2014. Mechanism associated with nonstructural carbohydrate accumulation in submergence tolerant rice (*Oryza sativa* L.) cultivars. *Journal of Plant Interactions*, **9**, 62–68.
Parida A K, Das A B. 2005. Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety*, **60**, 324–349.
Pearce R S. 2001. Plant freezing and damage. *Annals of Botany*, **87**, 417–424.
Piveta L B, Roma-Burgos N, Noldin J A, Viana V E, de Oliveira C, Lamego F P, de Avila L A. 2020. Molecular and physiological responses of rice and weedy rice to heat and drought stress. *Agriculture*, **11**, 9.
Posmyk M M. 2016. Exogenous melatonin improves antioxidant defence in cucumber seeds (*Cucumis sativus* L.) germinated under chilling stress. *Frontiers in Plant Science*, **7**, 575.
Pourrut B, Jean S, Silvestre J, Pinelli E. 2011. Lead-induced DNA damage in *Vicia faba* root cells: Potential involvement of oxidative stress. *Mutation Research/Genetic Toxicology and Environmental Mutagenesis*, **726**, 123–128.
Prince S J, Beena R, Gomez S M, Senthivel S, Babu R C. 2015. Mapping consistent rice (*Oryza sativa* L.) yield QTLs under drought stress in target rainfed environments. *Rice*, **8**, 1–13.
Qari S H, Hassan M U, Chattha M U, Mahmood A, Naqve M, Nawaz M, Barbanti L, Alahdal M A, Aljabri M. 2022. Melatonin induced cold tolerance in plants: Physiological and molecular responses. *Frontiers in Plant Science*, **13**, 843071.
Radha B, Sunitha N C, Sah R P, Azharudheen M T P, Krishna G, Umesh D K, Thomas S, Anilkumar C, Upadhyay S, Kumar A. 2023. Physiological and molecular implications of multiple abiotic stresses on yield and quality of rice. *Frontiers in Plant Science*, **13**, 996514.
Rang Z, Jagadish S, Zhou Q, Craufurd P, Heuer S. 2011. Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. *Environmental and Experimental Botany*, **70**, 58–65.
Rascio N, Navari-Izzo F. 2011. Heavy metal hyperaccumulating plants: How and why do they do it? And what makes them so interesting? *Plant Science*, **180**, 169–181.
Raza A, Charagh S, Najafi-Kakavand S, Abbas S, Shoaib Y, Anwar S, Sharifi S, Lu G, Siddique K H. 2023. Role of phytohormones in regulating cold stress tolerance: Physiological and molecular approaches for developing cold-smart crop plants. *Plant Stress*, **8**, 100152.
Ben Rejeb I, Pastor V, Mauch-Mani B. 2014. Plant responses to simultaneous biotic and abiotic stress: Molecular mechanisms. *Plants*, **3**, 458–475.
Rejeth R, Manikanta C L, Beena R, Stephen R, Manju R, Viji M. 2020. Water stress mediated root trait dynamics and identification of microsatellite markers associated with root traits in rice (*Oryza sativa* L.). *Physiology and Molecular Biology of Plants*, **26**, 1225–1236.
Reshma M, Beena R, Viji M, Manju R, Roy S. 2021. Validation of temperature induction response technique on combined effect of drought and heat stress in rice (*Oryza sativa* L.). *Journal of Crop and Weed*, **17**, 119–128.
De Las Rivas J, Barber J. 1997. Structure and thermal stability of photosystem II reaction centers studied by infrared spectroscopy. *Biochemistry*, **36**, 8897–8903.
De Ronde J, Cress W, Krüger G, Strasser R, Van Staden J. 2004. Photosynthetic response of transgenic soybean plants, containing an *Arabidopsis P5CR* gene, during heat and drought stress. *Journal of Plant Physiology*, **161**, 1211–1224.
Samarah N H. 2005. Effects of drought stress on growth and yield of barley. *Agronomy for Sustainable Development*, **25**, 145–149.
Dos Santos T P, Lopes C M, Rodrigues M L, de Souza C R, Ricardo-da-Silva J M, Maroco J P, Pereira J S, Chaves M M. 2007. Effects of deficit irrigation strategies on cluster microclimate for improving fruit composition of Moscatel field-grown grapevines. *Scientia Horticulturae*, **112**, 321–330.
Schutzendubel A, Polle A. 2002. Plant responses to abiotic stresses: Heavy metal-induced oxidative stress and protection by mycorrhization. *Journal of Experimental Botany*, **53**, 1351–1365.
Seo D H, Seomun S, Choi Y D, Jang G. 2020. Root development and stress tolerance in rice: The key to improving stress tolerance without yield penalties. *International Journal of Molecular Sciences*, **21**, 1807.
Shaheen T, Riaz M S, Zafar Y. 2016. Soybean production and drought stress. In: *Abiotic and Biotic Stresses in Soybean Production*. Elsevier, London. pp. 177–196.
Shavrukov Y, Kurishbayev A, Jatayev S, Shvidchenko V, Zotova L, Koekemoer F, De Groot S, Soole K, Langridge P. 2017. Early flowering as a drought escape mechanism in plants: How can it aid wheat production? *Frontiers in Plant Science*, **8**, 1950.

Shelden M C, Roessner U, Sharp R E, Tester M, Bacic A. 2013. Genetic variation in the root growth response of barley genotypes to salinity stress. *Functional Plant Biology*, **40**, 516–530.
Sherin G, Aswathi K R, Puthur J T. 2022. Photosynthetic functions in plants subjected to stresses are positively influenced by priming. *Plant Stress*, **4**, 100079.
Shi H, Ishitani M, Kim C, Zhu J K. 2000. The *Arabidopsis thaliana* salt tolerance gene *SOS1* encodes a putative Na^+/H^+ antiporter. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 6896–6901.
Shinozaki K, Yamaguchi-Shinozaki K. 2007. Gene networks involved in drought stress response and tolerance. *Journal of Experimental Botany*, **58**, 221–227.
Singh V, Singh A K, Raghuvanshi T, Singh M K, Singh V, Singh U. 2017. Influence of boron and molybdenum on growth, yield and quality of cauliflower (*Brassica oleracea* L. var. botrytis). *International Journal of Current Microbiology and Applied Sciences*, **6**, 3408–3414.
Sinha R, Zandalinas S I, Fichman Y, Sen S, Zeng S, Gómez-Cadenas A, Joshi T, Fritschi F B, Mittler R. 2022. Differential regulation of flower transpiration during abiotic stress in annual plants. *New Phytologist*, **235**, 611–629.
Smertenko A, Dráber P, Viklický V, Opatrný Z. 1997. Heat stress affects the organization of microtubules and cell division in *Nicotiana tabacum* cells. *Plant, Cell & Environment*, **20**, 1534–1542.
Song S, Li X, Tian Y, Zhou X, Qu Z, Liu J, Dong S. 2023. Physiology and proteomics analyses reveal the regulatory mechanism of mepiquat chloride in soybean. *Frontiers in Sustainable Food Systems*, **7**, 1188159.
Takahashi D, Li B, Nakayama T, Kawamura Y, Uemura M. 2013. Plant plasma membrane proteomics for improving cold tolerance. *Frontiers in Plant Science*, **4**, 90.
Taleisnik E, Rodríguez A A, Bustos D, Erdei L, Ortega L, Senn M E. 2009. Leaf expansion in grasses under salt stress. *Journal of Plant Physiology*, **166**, 1123–1140.
Tangpremsri T, Fukai S, Fischer K. 1995. Growth and yield of sorghum lines extracted from a population for differences in osmotic adjustment. *Australian Journal of Agricultural Research*, **46**, 61–74.
Tester M, Davenport R. 2003. Na^+ tolerance and Na^+ transport in higher plants. *Annals of Botany*, **91**, 503–527.
Tiryaki I. 2016. Drought stress and tolerance mechanisms in alfalfa (*Medicago sativa* L.). **19**, 296–304.
Turner N C, Wright G C, Siddique K. 2001. Adaptation of grain legumes (pulses) to water-limited environments. *Advances in Agronomy*, **71**, 193–231.
Tuteja N, Gill S S. 2016. *Abiotic Stress Response in Plants*. John Wiley & Sons, Italy.
Uzu G, Sobanska S, Aliouane Y, Pradere P, Dumat C. 2009. Study of lead phytoavailability for atmospheric industrial micronic and submicronic particles in relation with lead speciation. *Environmental Pollution*, **157**, 1178–1185.
Verbruggen N, Hermans C, Schat H. 2009. Molecular mechanisms of metal hyperaccumulation in plants. *New Phytologist*, **181**, 759–776.
Verma J K, Wardhan V, Singh D, Chakraborty S, Chakraborty N. 2018. Genome-wide identification of the Alba gene family in plants and stress-responsive expression of the rice Alba genes. *Genes*, **9**, 183.
Vierling E. 1991. The roles of heat shock proteins in plants. *Annual Review of Plant Biology*, **42**, 579–620.
Vu J C, Gesch R W, Pennanen A H, Hartwell Jr L A, Boote K J, Bowes G. 2001. Soybean photosynthesis, Rubisco, and carbohydrate enzymes function at supraoptimal temperatures in elevated CO_2. *Journal of Plant Physiology*, **158**, 295–307.
Wahid A, Shabbir A. 2005. Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. *Plant Growth Regulation*, **46**, 133–141.
Walter J. 2018. Effects of changes in soil moisture and precipitation patterns on plant-mediated biotic interactions in terrestrial ecosystems. *Plant Ecology*, **219**, 1449–1462.
Wang D Z, Jin Y N, Ding X H, Wang W J, Zhai S S, Bai L P, Guo Z F. 2017. Gene regulation and signal transduction in the ICE-CBF-COR signaling pathway during cold stress in plants. *Biochemistry* (Moscow), **82**, 1103–1117.
Wang L, Yin Y, Wang L F, Wang M, Zhao M, Tian Y, Li Y F. 2020. Transcriptome profiling of the elongating internode of cotton (*Gossypium hirsutum* L.) seedlings in response to mepiquat chloride. *Frontiers in Plant Science*, **10**, 1751.
Wang P, Sun X, Chang C, Feng F, Liang D, Cheng L, Ma F. 2013. Delay in leaf senescence of *Malus hupehensis* by long-term melatonin application is associated with its regulation of metabolic status and protein degradation. *Journal of Pineal Research*, **55**, 424–434.
Wani S H. 2018. *Biochemical*, *Physiological and Molecular Avenues for Combating Abiotic Stress in Plants*. Academic Press, Cambridge, USA.
Wei W, Li Q T, Chu Y N, Reiter R J, Yu X M, Zhu D H, Zhang W K, Ma B, Lin Q, Zhang J S. 2015. Melatonin enhances plant growth and abiotic stress tolerance in soybean plants. *Journal of Experimental Botany*, **66**, 695–707.
Wilson J, Ludlow M, Fisher M, Schulze E. 1980. Adaptation to water stress of the leaf water relations of four tropical forage species. *Functional Plant Biology*, **7**, 207–220.
Wu Y, Liu J, Wu H, Zhu Y, Ahmad I, Zhou G. 2023. The roles of mepiquate chloride and melatonin in the morpho-physiological activity of cotton under abiotic stress. *International Journal of Molecular Sciences*, **25**, 235.
Xiong D, Yu T, Ling X, Fahad S, Peng S, Li Y, Huang J. 2014. Sufficient leaf transpiration and nonstructural carbohydrates are beneficial for high-temperature tolerance in three rice (*Oryza sativa*) cultivars and two nitrogen treatments. *Functional Plant Biology*, **42**, 347–356.
Xiong L, Schumaker K S, Zhu J K. 2002. Cell signaling during cold, drought, and salt stress. *The Plant Cell*, **14**, S165–S183.
Yadav S, Modi P, Dave A, Vijapura A, Patel D, Patel M. 2020. Effect of abiotic stress on crops. *Sustainable Crop Production*, **3**, 5–16.
Yadav S, Sharma K D. 2016. Molecular and morphophysiological analysis of drought stress in plants. *Plant Growth*, **10**, 65246.
Yadav S, Vijapura A, Dave A, Shah S, Memon Z. 2019. Genetic diversity analysis of different wheat [*Triticum aestivum* (L.)] varieties using SSR markers. *International Journal of Current Microbiology and Applied Sciences*, **8**, 839–846.
Yang X, Wang B, Chen L, Li P, Cao C. 2019. The different influences of drought stress at the flowering stage on rice physiological traits, grain yield, and quality. *Scientific Reports*, **9**, 3742.
Zaman E, Karim M A, Bari M N, Akter N, Ahmed J U. 2016. Growth and yield performance of selected wheat varieties under water deficit conditions. *Bangladesh Journal of Scientific Research*, **29**, 163–172.
Zhang H, Liu L, Wang Z, Feng G, Gao Q, Li X. 2021. Induction of low temperature tolerance in wheat by pre-soaking and parental treatment with melatonin. *Molecules*, **26**, 1192.
Zheng Y, Wang Z, Sun X, Jia A, Jiang G, Li Z. 2008. Higher salinity tolerance cultivars of winter wheat relieved senescence at reproductive stage. *Environmental and Experimental Botany*, **62**, 129–138.

Executive Editor-in-Chief Xueyong Zhang
Managing Editor Ning Wang