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REVIEW ARTICLE

Strategies for adaptations and mitigation of abiotic stresses in crops: A review

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Abstract

Globally, we are fronting environmental pollution with augmented greenhouse gases which are the foremost ground of climate variation. Abiotic stresses i.e., drought, flood, heat, cold, salinity, ozone, heavy metal, and high irradiance are responsible for their detrimental influences on crop plants. A significant impact on plant distribution, growth and development, and agricultural productivity is imposed by abiotic stresses. As plants are sessile, they must deal with abiotic challenges as plants withstand these abiotic stresses by modifying morphological, physiological, and biochemical retorts. Addressing and mitigating these stresses are essential for ensuring sustainable agriculture. This review highlights the advancements in strategies to enhance crop adaptation and mitigation under abiotic stress conditions. Prominent approaches include developing stress-resilient crop varieties through traditional breeding methods and genetic engineering, employing bio-stimulants, phytochelatins, and plant growth regulators, and adopting innovative irrigation and soil management techniques. Emphasis is placed on molecular-level adaptations, such as modulating stress-responsive genes and strengthening antioxidant defense systems, for their role in boosting crop resilience. By consolidating recent progress and identifying research gaps, this review aims to establish a comprehensive framework for enhancing crop productivity amidst escalating environmental challenges.

Keywords: Abiotic stresses, drought, salinity, high irradiance, ozone, crop, plants mitigation

Introduction

In recent years, global warming has been the main cause of increasing temperature and different constituents are already veracity. Agricultural practices immensely rely on climatic conditions. Modern agricultural practices face abiotic stresses i.e., drought, exorbitant temperatures, salinity, nutritional deficiency, chemical pollutants, and oxidative stress turned out tobe the main environmental pressure. Agricultural crops interact with different environmental conditions and if these conditions exceed the critical limits, plants' normal growth and development become affected and impose stress. The core stress i.e., abiotic stresses that include drought, high salt stress, and low and high temperatures perniciously impacts the survival, of the production of biomass and staple crops yield up to 70%. Therefore, a menace to food safety all around the world, and important steps should be taken to improve the adaptation methods and mitigate agricultural systems.

Plant physiology and metabolic changes are species-specific responses that may be reversible or permanent with the imposition of abiotic stresses (Bhattacharyya *et al*. 2020). These responses may be influenced by the phenological stage, the intensity and severity of the stress, as well as the tissue or specific portion of the tissue/organ participating in the compensatory mechanism or stress (Seymen, 2021).

Plants have multiple systems for adaption or acclimatization to environmental pressures; hence, investigating the mechanism(s) by which plants receive stress indications, retort and adjust to these are biologically essential for understanding the complex regulatory processes of stress. This comprehension would enable scientists the develop superior crop varieties with enhanced stress tolerance.

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Plants modify numerous signaling pathways of metabolism to reduce the impact of diverse stresses on morpho-physiologically, biochemically and at the molecular level for acclimatization in varying climatic and environmental conditions (Fig. 1) (Fernie *et al.*, 2020). How well a plant responds to stress is determined by its ability to rearrange metabolic complexes, resume active growth and seed production (Fig. 2) and re-establish the osmotic adjustment with the elimination of stress.

Plants produce a wide variety of metabolites, such as carbohydrates, amino acids, phenolics, polyols, polyamines, lipids and others, that are geographically, temporally, and/or environmentally dependent (Fang *et al.*, 2019). Plants require primary metabolites, such as sugar molecules, intermediates of the TCA cycle, or amino acids for growth. Secondary metabolites, such as phenolics, nitrogen-containing chemicals, or terpenes, are required for the maintenance of plant-environment relationships. Different hormones, such as ethylene, abscisic acid (ABA), salicylic acid, or jasmonic acid (JA) regulate cellular growth and development, other features and performance of plants under stress.

Recently, it has been hypothesized that certain secondary metabolites function diversely and may operate as plant regulatory chemicals or hormones, influencing plant growth and development processes as well as pathogen defense. At the global scale, heat stress, drought, and salinity

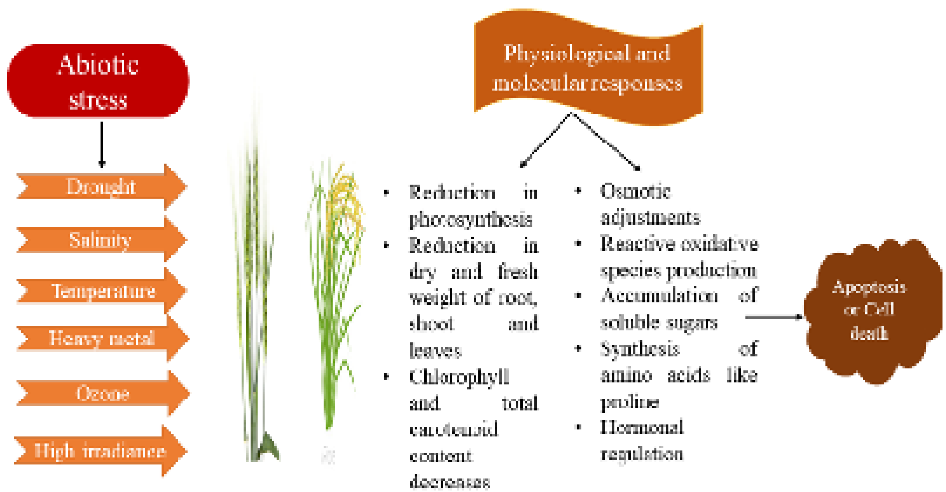

Figure 1: Physiological and molecular implications of crop plants in response to abiotic stresses

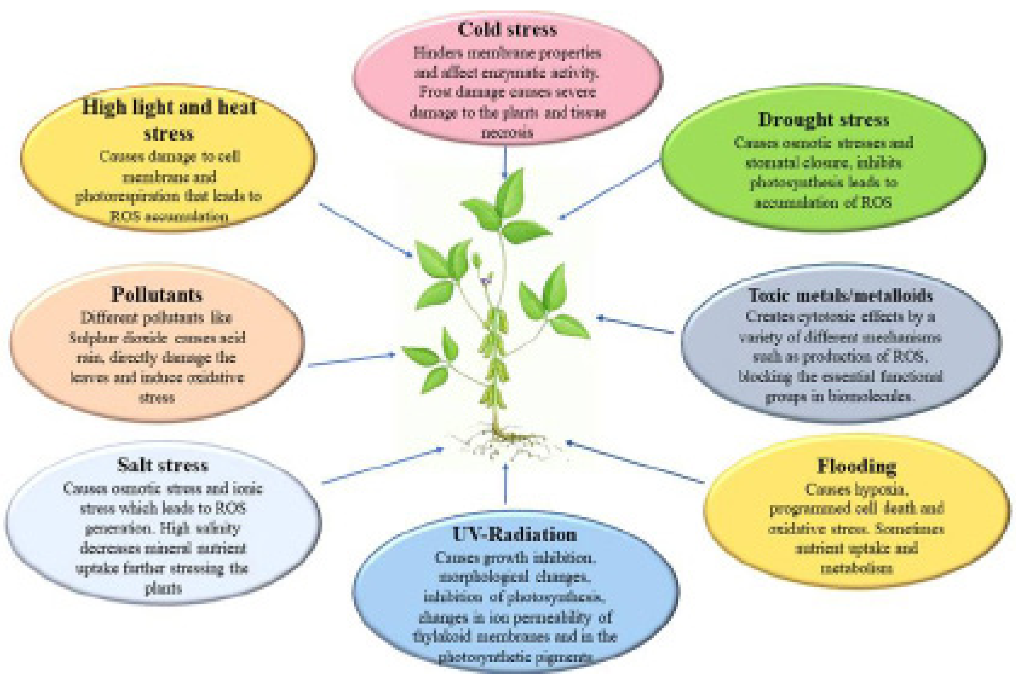

Figure 2: Figure showing an overview of various abiotic stresses—such as drought, flood, salinity, extreme temperatures, and heavy metals—and their adverse effects on plant growth, development, and productivity.

are the primary abiotic variables that have adverse impacts on crop production; however, their impacts differ by region. Drought, high temperatures, and salinity stress induce all the same biochemical and physiological changes in growing plants, resulting in identical symptoms. Osmotic stress is a common consequence of salinity, dehydration, and high temperatures. Despite the plethora of studies conducted in recent years, we still have a limited understanding of how plants respond to key abiotic challenges. This review will include the most up-to-date information on the primary abiotic stresses (drought, flooding, salinity, heat stress, cold, ozone, heavy metal, and high irradiance) faced by current agricultural practices, along with responses performed by plants against these stresses.

Plants responses to drought and mitigation strategies

Drought is an environmental state marked by under-average rainfall rates for extended durations, resulting in lower water content in soil i.e. accessible for agricultural growth and development. Water stress is noteworthy from an agronomic standpoint because it influences crop performance, particularly when it occurs during the crucial period of times during the growing season. Drought stress costs billions of dollars worldwide, notably in dry and semi-dry countries. Drought events occur more frequently due to less precipitation, not only due to the high temperature but also due to the exorbitant and crazy usage of resources that are naturally present and the desertification of soils. Plants have developed drought defense mechanisms that differ depending on the lineages and the severity or duration of the drought. The water potential of the leaf, osmotic adjustment (OA), the maximal quantum yield of PSII (Fv/Fm), water usage efficiency (WUE), the integrity of the cell membrane, and relative water content (RWC) are all physiological measures linked to the availability of water and could be used as water stress indices. Plants are usually distressed by the scarcity of water or drought when the water of the soil becomes inaccessible for rates of transpiration and evaporation is too high. During drought stress, there is a drop in the turgor pressure of cells which causes the reduction in leaf water potential and related processes (such as stomatal closure), that means prevents the loss of H_2O content and absorption of nutrients (Escalante-Magaña *et al*., 2019). While, according to various studies, tolerance against drought is not necessarily linked to the maintenance of the turgor potential of leaves (Rubin *et al*., 2017). Osmotic adjustment by the build-up of osmolytes is one of the initial reactions of plants under drought stress. Osmolytes and osmoprotectants are minute, electrically neutral substances that have no harmful effects at molar quantities and protect membranes and proteins from abiotic stress-induced denaturation. Furthermore, osmolytes accumulating in the compartments of the cytoplasm are critical for maintaining the turgor pressure of cells. Plants seek to raise the solute potential at the cellular level to overcome adverse effects under abiotic stress circumstances by integrating and agglomerating osmolytes such as proteins, glycine betaine (GB), soluble carbohydrates, free amino acids and proline (Pro). One important indicator of a plant's ability to withstand temperature and water stress is pro accumulation. It buffers the effects of drought by maintaining water potential as an osmolyte. Plant proteins can undergo qualitative and quantitative alterations as a result of drought stress. Protein modifications have been observed in plants like *Zea mays* and *Lycopersicon pennellii*.

To protect cells from drought, LEA proteins, HSPs and osmotines are secreted by plants (Priya *et al*., 2019). LEA proteins belong to the 'hydrophilins' family of proteins that safeguard other proteins from osmotic stress. HSPs aid in the binding, folding, displacement and degradation of different proteins (Ohama *et al*., 2017). Osmotines, rather, are the proteins that safeguard cells from osmolarity and structural-metabolic disturbances (Le *et al*., 2018). It has been found that when sunflower plants are deprived of water, their leaf-soluble proteins fall, but in other discoveries, it has been observed that drought resistance in crops is linked to greater protein levels. The number of soluble proteins in a plant depends on the species and kind of tissue under water stress. Dehydrins' effect on water scarcity has been thoroughly researched. Dehydrins are involved in confiningions, regulating the concentration of solute in the cytoplasm during dry circumstances, and the osmotic adjustment. Osmotin (molecular weight: 24 kDa) is a protein i.e., rich in cysteine amino acid, that protects cell membranes from dehydration. It has been discovered that osmotin enhances drought tolerance transgenic expression with the rd29A promotor in mulberry plants. Accordingly, overexposure of the osmotin gene in transgenic tomato plants improves drought tolerance. A work using transgenic bentgrass expressing RSOsPR10 demonstrated that osmotin promotes drought resistance by preserving the photosynthetic mechanism. Whereas the acquired sunlight could not be completely transformed into chemically bound energy during drought stress, the photosynthetic rate slows, and the excess energy causes photo inhibition. Fv/Fm represents the maximum potential quantum efficiency of PS-II can be used to distinguish between genotypes that are resistant or sensitive to H_2O stress. When resistant genotypes of tomato were exposed to water stress, for example, maintained a high PSII expression as well as consequently increased activity of photosynthesis than sensitive genotypes (Chatterjee and Solankey, 2015).

Early-season drought stress is more harmful than late-season water deficiency. In many crops, seed priming is a highly efficient way to increase germination, emergence, and seedling vigor. Hydro-priming (using water) is the simplest technique to increase germination; but, under stress, researchers found that osmo-priming such as halo-priming, hormonal priming and chemo-priming is very efficient for increased seedling vigor. Much of the damage under abiotic conditions like water stress happens at the cellular level and antioxidant defense arises because of oxidative damage. By seed priming with an osmoprotectant, nucleic acids are repaired and protected, protein synthesis is increased and cellular membranes are also repaired.

Drought effects on wheat have been successfully mitigated by applying growth stimulants, osmoprotectants and antioxidants. Plants primed with cytokinins produce more chlorophyll (Chl), accumulate more biomass, and have faster photosynthetic rates, more stable membranes and maintain ionic status. Similar findings were made, and they claimed that priming soybean seeds with cytokinins (Benzyl adenine) improved the biomass of roots, flowering, and fruiting in stressed plants. Seeds of *Arabidopsis* primed with amino-butyric acid improved drought tolerance by ABA accretion and closure of stomata. However, it is unknown how ABA-primed seeds affect plant stomatal regulation.

Foliar treatment is particularly effective because plants can easily access the compounds delivered by foliar sprays. Production of reactive oxygen species occurs in wheat under extreme drought conditions. The foliar application of minerals like magnesium, calcium, potassium and vitamin A helps scavenge the reactive oxygen species in wheat. Several scientists have successfully used a foliar spray of potassium on wheat leaves to mitigate drought stress. GAs applied exogenously can alleviate abiotic stressors and recover plant growth and development. Application of GA_3exogenously enhanced the growth of wheat plants and alleviated oxidative harm prompted by drought stress. Exogenous silicon (Si) application in wheat and rice is also effective in reducing the impact of drought stress. Si treatment exhibited increased antioxidative activity, enhanced photosynthetic pigments and altered gene expression in the ascorbate-reduced glutathione cycle. The application of SA to water-deficit-stressed plants through foliar spraying helps alleviate negative effects by minimizing H_2O_2 accumulation and lipid production. SA is widely recognized for its role in mitigating stress-related damage and influencing key physiological pathways in plants (Kumar *et al*., 2023).

Plant Responses to Flooding and Mitigating strategies

The severity of flooding disasters is growing as a result of global warming and climate change, as irregular rainfall becomes more common and sea levels rise due to the melting of glaciers. Flooding is a common environmental stress that destroys the natural distribution of plants and has a catastrophic effect on the growth of crops and food output. It has been found that the amount of O_2 available for the roots becomes lower due to flooding. It also limits the deep-water diffusion of the gas. The pace of photosynthesis under the water (relies on the levels of light and CO_2 accessibility), the appearance of leaves in different forms, the existence of gas layers, shoot cells rate of respiration and the concentration of O_2 in the layer of water all influence endogenous O_2 levels. Reciprocation of gases is essential for photosynthesis and respiration in plants. Aerenchyma development, external roots, shoot elongation, and increased shoot biomass are some of the mechanisms that plants engage to reduce the consequences of oxygen deprivation during floods. Plant cells must develop/rely on alternate metabolic routes to make ATP in such anoxic circumstances due to the down-regulation of ways of metabolic pathways and energy and suppression of mitochondrial respiration. The pathway of glycolysis generates 2 molecules of ATPs and 2 molecules of pyruvate/unit of the glucose molecule, although NAD^+ is reduced to 'NADH' under anoxic conditions. The process of fermentation uses substrate i.e., pyruvate for the metabolism and the enzyme lactate dehydrogenase produces lactic acid or the production of ethanol catalyzed by the enzymes 'pyruvate decarboxylase' and 'alcohol dehydrogenase'.

Increased flooding and poorly drained, soggy soils are the results of climate change, altering the hydrological cycle in several parts around the world, which has a detrimental impact on crops by limiting oxygen levels for roots and microbes present in the soil. An exhaustive review comes to the conclusion that plants try to sustain their interior homeostasis by balancing the hormonal crosstalk under the stress of excessive water and providing an escape and resilience option under flooding stress. In addition, some treatments have been proven to improve plant performance when exposed to the stressful effects of water logging. One such therapy is seed priming with sodium azide (NaN_3).

With flood tolerance, the antioxidant defense system is frequently up regulated. It was shown that plant soybean has been subjected to anoxic stress for two hours raised the amount of superoxide dismutase (SODs); however, subjecting the same to anoxia for five hours (anoxia) improved its resistance to free oxygen radicals and resulted in minimum damage. Externally provided ascorbic acid (ASA) incubation reduced post-anoxic damage in the roots of soybean. Wheat and *Hordeum vulgare* roots and leaves displayed H_2O_2 build-up in anoxic environments.

Similarly, the activity of glutathione reductase increased, and the content of glutathione in wheat seedlings mitigated post-hypoxia oxidative stress. In anoxic conditions, wheat plants lowered the activity of several enzymes. A recent study showed transcriptome differences between flood-tolerant and flood-sensitive maize genotypes through the activation of tolerant genes involved in the fermentation pathway and antioxidant defenses. After 6 days of flooding, genotypes of pigeon peas, i.e., flood-tolerant, demonstrated an unceasing increase in antioxidant activity; in contrast, sensitive genotypes showed a decline in antioxidant activity after 48 hours of water logging.

Plants responses to heat Stress(high temperature) and mitigation strategies

It has been predicted that global temperature has increased by 0.8˚C since 1975. The level of CO_2 and other greenhouse gases increased with the rise in temperature. Plants exposed to high temperatures go through a variety of alterations and modifications. Plant species around the world react to temperature changes differently, specifically in terms of crop productivity (Bashandy and El-Shaieny, 2021). Elevated and prolonged high temperatures cause cellular damage in plants by altering proteins, nucleic acids, enzymes, and membranes, leading to cell mortality. Heat stress can be direct, such as protein denaturation and membrane fluidity changes, or indirect, like enzyme inactivation and loss of membrane integrity. These alterations disrupt cellular processes, causing severe damage in minutes. Plants respond by adapting their morphology, such as growing deeper roots, reducing stomata, and thinning leaves to minimize water loss (Goufo *et al*., 2017). Heat stress also impacts cellular structures, such as cell walls and starch content, and can impair photosynthesis and metabolism by damaging membranes and proteins (Jacob *et al*., 2017).

Plants sense heat stress through calcium channels and various proteins, triggering protective responses. High temperatures decrease leaf water potential, stomatal conductance, and photosynthesis by damaging thylakoid membranes and reducing photosynthetic pigments and PSII activity. Reactive oxygen species (ROS) production increases, leading to oxidative stress and damage to plasma membranes, proteins, and root growth (Hasanuzzaman *et al*., 2013). Heat stress is particularly detrimental during flowering and reproduction, where it can reduce grain production or cause floral abortion.

Plants employ various heat stress avoidance mechanisms, such as adjusting leaf orientation, closing stomata, increasing stomatal density, and altering membrane lipids. To protect against heat, some plants grow tomentose hairs on leaf surfaces. Smaller leaves are more heat-tolerant than larger ones due to reduced surface hindrance during heat release. Plants also aim to complete their reproductive cycle before heat stress peaks. In maize, for example, net photosynthesis drops when leaf temperatures exceed 38°C, especially with sudden temperature increases. This decline is linked to Rubisco inactivation; with higher temperatures leading to reduced activation and diminished photosynthesis (Rubisco acclimatization involves the synthesis of activase polypeptides).

It has been observed that heat exposure (45°C) caused fatalities to cells and harm to the embryo of wheat during the initial developmental stage (initial 6 days of growth. For example, heat stress reduced plant height in wheat and the first leaf growth has been impeded by prolonged exposure to high temperatures. It has been found that high temperature causes crucial water loss, which has a negative impact on the biomass output of *Jatropha curcas* for biofuel production. It has been observed that maize, wheat, mungbean, and chickpea all face heat-induced chlorosis. In crops such as cotton and rice, the negative impacts of heat stress throughout vegetative and reproductive growth phases have been explored utilizing agronomic, phenological, morphological, and physiological assessments. Tiller numbers were reduced but stem elongation was enhanced in wheat plants at high temperatures, especially at night. Treatment of maize with high temperatures (35/27°C Day/night) stimulated their vegetative growth and biomass output.

Cereals are subjected to different high-temperature stresses, which cause changes in plant growth and development. The exogenous application of brassinosteroids stimulates the development of protective components and reduces the impact of stress. The intensity, frequency, and duration of heat stress all vary. Plants established distinct coping mechanisms with the augmentation of heat stress. After being preconditioned to mildly high temperatures, plants can endure excessive temperatures through a process known as heat acclimation, also known as acquired thermos-tolerance. In wheat, for instance, acclimation to high temperatures at the pre-anthesis stage has been found to mitigate the deleterious effects of high temperatures during the anthesis and post-anthesis stages, increasing yields compared to non-acclimated plants.

High temperature is also diminished by the induction of osmoprotectants, with BR helping to increase the expression of these vital substances. Heat stress causes cellular membranes to become more unstable, which disrupts membrane permeability and electrolyte leakage, ultimately causing cell death and senescence. Under various unfavorable environmental conditions, osmoprotectants such as betaines, carbohydrates, and amino acids, including free proline, preserve the osmotic balance of cells.

Applying macronutrients like K and Ca, as well as micronutrients like boron, selenium, and manganese, which are known to alter the functions of stomata, activates the physiological and metabolic processes, helping in the maintenance of water potential in tissues and increase tolerance to stress of high temperature. The administration of nutrients like nitrogen, potassium, calcium, and magnesium has also been shown to increase the concentration of antioxidant enzymes in plant cells, decreasing ROS toxicity. The effects of temperature on several plants' photosynthetic systems are compiled in Table 1.

Table 1: The impact of heat and cold stress on plants' photosynthetic systems

Temperature stress	*Plant species*	*Effect on photosynthetic systems*	***References***
Heat stress	*Zea mays*	Function of RUBISCO activase ↓	(Salvucci *et al*. 2001)
		The rate of net photosynthesis inhibited, leading to the closure of stomata	(Crafts-Brandner and Salvucci, 2002)
Heat stress	*Gossypium barbadense*	The overall decline in photosynthesis due to the restricted activity of the photosynthetic electron transport system and ribulose- 1, 5 bisphosphate	(Wise *et al*., 2004)
Heat stress	*Triticum aestivum*	Decreased chlorophyll production, leading to the deterioration of enzymatic processes.	(Efeoglu and Terzioglu, 2009)
Heat stress	*Prosopis chilensis* & Prosopis tamarugo	Reduction in photosynthetic efficiency and photochemical performance	(Delatorre *et al*., 2008)
Heat stress	*Citrus medica*	Decrease in photochemical efficiency of PS II, chlorophyll fluorescence, photosynthetic electron transport, carboxylation and efficiency, photosynthetic capacity	(Chen *et al*., 2012b)
Heat stress	*Populus simonii*	Decreased electron transport, disruptions in the photosystems, and activation of the glycolate pathway led to H_2O_2 generation, causing damage to the entire photosynthetic apparatus.	(Song *et al*., 2014)
Cold stress	*T. aestivum*	Inhibition of photosynthesis	(Li *et al*., 2014)
Cold stress	*Hibiscus* rosa-*sinensis*	Decreased PS II quantum yield, electron transport, and photochemistry efficiency	(Paredes and Quiles, 2015)
Heat stress	Glycine max	Enhanced photosynthesis rates, mesophyll and stomatal conductance, photosystem II quantum yield, carboxylation rate, and electron transport across CO_2 levels	(Xu *et al*., 2016a)
Cold stress		The photo-biochemical process, followed by stomatal and mesophyll restrictions, limits photosynthetic activity. Buildup of organic acids and sugars that inhibits photosynthesis	
Cold stress	*Citrullus lanatus*	Decrease in chlorophyll content, net photosynthetic rate, intercellular CO_2, stomatal conductance,	(Hou *et al*., 2016)
Heat stress	*Cucumis sativus*	Reduced starch content, photochemical quenching coefficient, net photosynthetic rate, and actual photochemical efficiency	(Ding *et al*., 2016)
Heat stress	*T. aestivum*	decrease in PS II's photochemical activity and chlorophyll concentration	(Chen *et al*. 2017a)
Heat stress	Pisum sativum	Reduced carbon dioxide assimilation, lower stomatal conductance, and diminished water use efficiency.	(Abdulmajeed *et al*., 2017)
Cold stress	*Lycopersicone-sculentum*	net photosynthetic rate decreased	(Liu *et al*., 2017)
Cold stress	*Oryza sativa*	Reduction in chlorophyll content, net photosynthetic rate, intercellular CO_2, stomatal conductance, and maximal photochemical efficiency of PS II (*F*v/*F*m)	(Han *et al*., 2017)
Cold stress	*L. esculentum*	Damage to the thylakoid membrane, decreased light energy distribution, and a reduced electron transport rate.	(Yang *et al*. 2018)
Cold stress	*Saccharum officinarum*	Alteration of chloroplast structure, a decrease in microtubules and grana lamellae within the chloroplast, and a decline in overall photosynthetic efficiency.	(Li *et al*. 2018a)
Cold stress	Camellia sinensis	Decrease in net photosynthetic rate, intercellular CO_2, stomatal conductance, transpiration rate, and maximal photochemical efficiency of PS II	(Li *et al*., 2018b)
Cold stress	*T. aestivum*	Reduction in photosynthesis due to damaged membrane of thylakoids	(Djanaguiraman *et al*., 2018)
Heat stress		Reduction in stomatal conductance and the rate of CO_2 absorption	(Hlaváčová *et al*., 2018)
Heat stress		damaged thylakoid membrane and decline net photosynthetic rate	(Djanaguiraman *et al*., 2018)
Cold stress	*Lycopersicon esculentum*	Reduction in chlorophyll content, leaf area, net photosynthetic rate, stomatal conductance, intercellular CO_2, transpiration rate,Decline in expression of proteins involved in photosynthesis	(Khan *et al*.,2019)

Plant responses to cold stress and mitigation strategies

Cold stress is a major abiotic factor that reduces agricultural productivity by affecting crop quality and post-harvest life. Plants must adapt their metabolism to endure low temperatures as they are immobile. Cold acclimation, the process through which temperate plants develop resistance to chilling and freezing stress, plays a crucial role in this adaptation. However, plants vary in their tolerance to cold, with crops from tropical and subtropical regions, such as maize, cotton, and rice, being more susceptible to freezing. In contrast, plants in temperate regions can tolerate low temperatures to varying degrees. Their resistance is not innate but results from biochemical and physiological adjustments, such as the ability to withstand freezing after acclimatization. For example, rye can survive temperatures as low as -30°C after 7 to 14 days of acclimation at 2°C, but unacclimatized rye cannot survive -5°C.Cold stress affects nearly all aspects of plant biology, and research into cold adaptation has revealed that plants activate both enzymatic and non-enzymatic antioxidative mechanisms to cope with chilling temperatures. They produce osmolytes like proline, glycine betaine, and carbohydrates to protect against chilling injury, such as plasma membrane damage. Additionally, genes and proteins are involved in cold acclimation, enhancing freezing resistance. In hexaploid wheat, all chromosomes contribute to resistance against chilling injury. Key components of cold stress signaling include Ca2+, reactive oxygen species (ROS), protein kinases, protein phosphatases, and lipid signaling. ABA also plays a crucial role in mediating the cold stress response. Plant responses to cold stress vary depending on gene expression that influences their metabolism, physiology, and growth, highlighting the complexity of cold stress mechanisms. The cold response mechanism could be linked to different alterations such as the expression of different kinases in signal transduction, osmolytes accumulation and membrane lipid composition (Fig. 3).

Plant hormones (phytohormones) are small molecules that regulate various cellular processes in plants, acting as chemical messengers to convey activity. They help plants cope with abiotic stressors like drought, salt, and chilling temperatures, triggering responses that increase adaptability. Examples include auxin, ethylene, gibberellic acid (GAs), cytokinins (CKs), jasmonic acid (JA), brassinosteroids (BRs), abscisic acid (ABA), strigolactones, and salicylic acid (SA). Genetic and biochemical studies have revealed that these hormones are crucial in cold stress tolerance. Auxin, especially in the form of IAA, is vital for plant development and cold resistance, with low temperatures increasing OsYUCCA expression and enhancing IAA content in rice. Abscisic acid (ABA) is another critical hormone for stress response, with ABA deficiency in *Arabidopsis* leading to reduced freezing tolerance. Cold stress elevates ABA levels, activating proteins like SnRK2, which are essential for stress signaling in plants, including wheat. Ethylene, a gaseous phytohormone, regulates processes like structural differentiation and stress responses. Cold stress affects ethylene levels in various plants, reducing production in *Arabidopsis* while increasing it in *Secale cereale*. In wheat, chilling stress activates ethylene-responsive factor 1 (ERF1), a key member of the ERF gene family. Gibberellins (GAs) play a key role in plant adaptability to abiotic stress, with DELLA proteins controlling GA-responsive growth. Cold stress increases DELLA accumulation by reducing GA levels and enhancing GA2-oxidase gene expression. CBF1 over-expression results in reduced bioactive GA, causing dwarfism and delayed blooming. This suggests that cold signaling affects both GA content and signaling, with DELLA regulating growth regulatory factors (GRFs) early in the cold stress response (Table 2).Jasmonic acid (JA) and methyl jasmonate (MJ) regulate plant stress responses. Cold stress in Arabidopsis induces JA biosynthesis genes like AOC1, LOX1, and AOS1, while JAZ proteins inhibit ICE1, promoting CBF expression. In wheat, cold increases TaJAZ expression and endogenous JA levels. Transgenic wheat with higher AtOPR3 expression shows increased JA and improved chilling tolerance (Hassan *et al*., 2021).Brassinosteroids (BRs) are key phytohormones for growth regulation and stress tolerance. Exogenous BR treatment enhances cold tolerance and gene expression of COR in *Arabidopsis* and promotes recovery in maize and cold tolerance in winter wheat and rye (Sadura, and Janeczko, 2021). In Arabidopsis, BIN2 (brassinosteroid insensitive 2) inhibits cold tolerance (Ye *et al*., 2019). To combat cold stress, plants accumulate soluble carbohydrates, like fructans, which stabilize membranes. In wheat, fructan buildup enhances cold resistance under low-temperature stress (Yokota *et al*. 2015). Carbohydrate accumulation during acclimatization helps plants tolerate chilling stress by

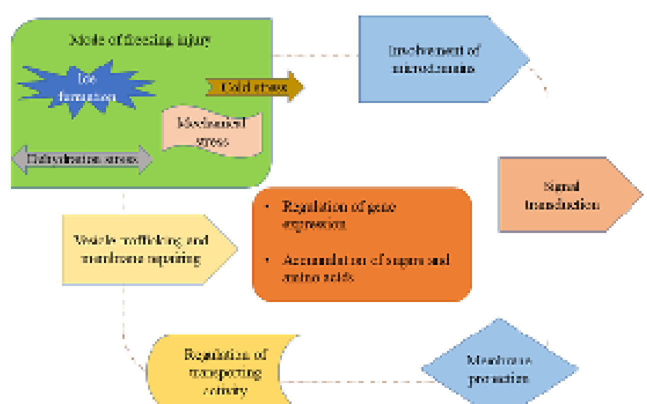

Figure 3: Mechanisms adaptedby the plants during cold acclimation. (Takahashi *et al*. 2013).

Table 2: Effect of exogenous application of plant growth regulators

Growth regulators	*Crop species*	*Concentration*	*Outcome*	*References*
Glycinebetaine (GB)	*Zea mays*	50, 100, and 150 mg	Higher biomass accumulation and growth rate of maize plants	Farooq *et al*. (2008)
Brassinosteroid (BR)	*Capsicum annuum*	5, 10, and 15 µM	membrane integrity is maintained due to reduced leakage of electrolytes and antioxidant activity increased	Wang *et al*. (2012)
Gibberellic acid (GA)	*Oryza sativa*	1 or 10 µM	Inhibited male sterility induced by cold stress and amended seed-setting rate	Sakata *et al*. (2014)
	Linum usitatissimum	10^{-6}M	Ameliorated the impact of salinity stress at its highest level (10 dSm^{-1}), increased root parameters while decreasing the osmotic potential (Ψs)	Yadav *et al*. (2024)
Salicylic acid (SA)	*Zea mays*	1 g	Improved photosynthetic efficiency, redox homeostasis, and total chlorophyll content	Waqas *et al*. (2017)
Thiourea	*Zea mays*	0.2 g	Dry matter, photosynthesis, water consumption, and growth rate ↑	
5-aminolevulinic acid (ALA)	*Oryza sativa*	8.5 mM	enhanced relative gene expression of the enzymes involved in PA biosynthesis, Improved POD, APX, SOD, and GPX activities;	Sheteiwy *et al*. (2017)
5-aminolevulinic acid (ALA)	*Zea mays*	0.15 mM	Proline build-up was increased, CAT, SOD and RuBP catalase activities were induced, and crop yield loss was avoided.; loss of crop yield prevented	Wang *et al*. (2018b)
5-aminolevulinic acid (ALA)	*Solanum lycopersicum*	25 mg	Reduced oxidative stress induced by cold by directly activating NO synthesis and mediating the interaction between JA and NO.	Liu *et al*. (2019)
24-epibrassinolide (24-EBL)	*Solanum lycopersicum*	10^{-8} M	enhanced proline, chlorophyll, and net photosynthetic rate; induced growth rate and biomass gain	Khan *et al*. (2019)
Polyamine (PA)	*Brassica napus*	1 mM	enhanced resistance to cold; sustained H+-ATPase activity in the plasma membrane; hindered ethylene emission stimulation	Jankovska *et al*. (2020)
Indole-3-acetic acid (IAA)	*Cucumis sativus*	75 µM	Enhanced photosynthetic enzymes (FBPase, RuBP, catalase) and ROS scavenging activity (APX, CAT, and SOD)	Zhang *et al*. (2020b)
Abscisic acid (ABA)	*Triticum aestivum*	100 µM	Enhanced ROS scavenging capacity through elevated antioxidant (CAT and SOD) activity	Yu *et al*. (2020)
Abscisic acid + calcium chloride (ABA + $CaCl_2$)	*Cucumis sativus*	35 µg + 500 mg	Increased expression of genes related to photosynthesis and metabolic processes; improved leaf area and ROS homeostasis	Feng *et al*. (2021)
Sodium hydrosulfide (NaHS)	*Cucumis sativus*	1 mM	Reduced electrolyte loss, H_2O_2 and O^{2-} buildup, and injury due to cold stress	Zhang *et al*. (2021b)
Melatonin (MT)	*Triticum aestivum*	1 µM	enhanced nitrogen absorption, nitrate reductase and glutamine synthetase activity, root/shoot ratio, and plant biomass production	Qiao *et al*. (2019)
Melatonin (MT)	*Hordeum Vulgare*	1 µM	Enhanced germination, seedling growth, proline, and soluble protein accumulation, chlorophyll and carotenoid content, and HvCCA1 and HvTOC1 gene expression.	Chang *et al*. (2021)

acting as osmoprotectants, ROS scavengers, and signaling molecules. Trehalose is also involved in modulating low-temperature tolerance, possibly through starch build-up. Studies show winter wheat maintains carbon absorption better than spring wheat at low temperatures due to higher sucrose biosynthetic enzymes. Additionally, winter wheat has higher carbohydrate content, aiding its resistance to cold stress, unlike spring wheat. Advanced molecular techniques can explore how sugars influence gene expression in cold environments. Photosynthesis and biomass accumulation are vital for the production of food and the growth of crops like wheat. However, these processes are highly sensitive to chilling stress, which is linked to decreased yield, reduced leaf area, smaller size, lower biomass, fewer spikes, and altered carbohydrate metabolism (Karimi *et al*., 2011). Chilling stress reduces photosynthetic efficiency, with a 45% decline in leaf photosynthetic rate compared to a control. Cold stress impairs photosynthesis by limiting stomatal conductivity, hindering chloroplast development, reducing chlorophyll synthesis, and inhibiting Rubisco activity during carbon assimilation. The electron transport chain is disrupted, and energy storage declines. Additionally, cold-induced drought stress lowers molecular oxygen levels and increases ROS, further damaging photosynthetic mechanisms. Reduced leaf area during the vegetative stage exacerbates the imbalance between carbon sources and sinks (Liu Y. *et al*., 2019). Cold shock at various growth stages decreases photo- assimilation and carbohydrate transport, resulting in significant yield reductions. Cold stress disrupts wheat plant respiration by impairing mitochondrial structure, reducing enzymatic activity, and limiting ATP synthesis. Sensitive plants show uneven respiration, while alternate pathways in corn and wheat help repair mitochondrial damage. These disruptions impact energy flow, photosynthesis, and overall growth (Feng *et al*., 2008; Ikkonen *et al*., 2020).In addition, cold is another frequent stressor that sets off complex processes that change the molecular makeup of cells to shield them from harm. Various treatments can lessen the harm caused by low temperatures. Chitosan, which improved the photosynthesis and carbon process in tea plants, or 5-Aminolevulinic, which improved the functioning of cucumbers, were both shown to lessen the impacts of cold stress in the plants that were studied. Additionally, the AsA improved the tomato's antioxidant resistance to low-temperature stress. When *T. aestivum* was subjected to the combination of both stresses i.e., herbicides and lower temperature (2 °C), the foliar spray of AsA reduced the MDA content and excess light (EL) in *T. aestivum* seedlings. This decreased oxidative damage caused by AsA may be the result of ROS scavenging during times of stress, as shown by AsA-intervened decreases in H_2O_2 and O_2 which were accredited to rising APX, PODand GR activities. Under low-temperature stress, the external administration of SA enhances the productivity of *Zea mays*. By limiting the production of H_2O_2 and lipid peroxidation, as well as by enhancing the activities of antioxidant enzymes including CAT, APX, and SOD, seed priming with SA lowered the abiotic stresses. Furthermore, seed priming increased the production of these osmolytes, much like glycine betaine and proline, which are essential in stress reduction. *Glomus mosseae*, an AM fungus, decreases the level of malondialdehyde, boosted soluble proteins, antioxidant enzymes activities i.e., POD, SOD, CAT and APX, and pigments of photosynthesis to decrease the stress caused by low temperatures on tomato plants (Inbaraj, 2021).

Plants responses to salinity and mitigation strategies

Soil is considered saline if it has a higher content of soluble salts i.e. when the osmotic pressures imposed by ions are identical to that exerted by 40 Mm NaCl (0.2 MPa). The salinity of soil is among the abiotic stresses that constrain the soil's ability to cultivate crops. Due to this, crop productivity becomes limited and cultivation is inhibited on the affected land. Presently, the world's 1/3rd of the cultivable area is afflicted by salinization. Salinity has ion-specific effects, imbalance of osmosis, and oxidative damage affects the development and growth of crops. There is a negative relationship between the salinity stress of soil and the productivity of crops. Salt concentrations, as usual, cause alteration in biochemical and physiological processes, limiting the growth and maturation of the plants' leaves, shoots, and roots. Salinity induces both osmotic and ionic stress in plants. Increased salt levels in the soil reduce the soil's ability to hold water, which reduces the amount of water that plant roots can absorb. Excessive ion accumulations such as Na^+ and Cl^- in cells, cause nutritional problems or toxicity in plants. The responses of crop plants to salt stress involve two major steps (I) the first one is an osmotic phase which is fast and occurs when roots capture salt. The ψ of soil becomes lowered and causes a decrease in the growth of the shoot because of reduced ψ_w; (II) the other phase is slower than the first one and involves the acquisition and transmission of harmful ions like sodium ions (Negrão *et al*., 2017). Cations like Ca^{2+}, Mg^{2+}, K^+, and Na^+, as well as anions like SO_4^{2-} Cl^-, $SO4^-$, HCO_3^-, CO_3^{2-}, and NO_3^- are implicated in salt stress signaling because cell homeostasis is achieved through their interaction (Tripathi and Muller, 2015).

Salt stress exposure causes the activation of an osmotic adjustment process to sustain cell turbidity, resulting in stressed plants' delayed development. Meanwhile, exposure of plants to salt stress, the alterations that result can differ depending on management and genotype, stages of development, period, and intensity of stress. Plants can respond to stress by triggering a variety of physiological and biochemical mechanisms, including modifications in external or internal structure, water relations, photosynthesis, phytohormones, ion circulation, and biochemical adjustment. Excessive salt concentrations in plant tissues can impede development and productivity by interfering with key processes like germination, balance of minerals, photosynthesis, and balance of redox reactions, among others. Salinity might affect the imbibition of seeds, and impact the germination medium by lowering the osmotic potential which influences germination and alters the enzymatic activity included in nucleic acid and protein metabolism. The impacts of salinity on germination may differ by cultivars and species, as well as levels of salt, Rice, wheat, maize, *Brassica* species, and tomato all demonstrate a negative association between the rate of germination and salinity.

Salinity inhibits photosynthesis by the reduction of water potential in plants and the production of chlorophyll. Cl^-, for instance, has been shown to inhibit chlorophyll synthesis (46.97%) and shows a reduction in crop output by 10% with 490 mg/kg Cl^- in the soil (Sawariya *et al*., 2024). The essential Cl^- levels for sensitive species can range from

4 to 7 mg g^{-1} and for tolerant species range from 15 to 50 mg/g, depending on the species. As observed in mung bean (*Vigna radiata*), salt can reduce the quantity of carotenoids and xanthophyll, as well as the intensity of chlorophyll fluorescence, with chlorophyll b being more vulnerable to salinity rise than chlorophyll a. In controlled environmental trials, wheat genotypes lost up to 82 percent of their grain yield in response to salt stress (Oyiga *et al*., 2016). In wheat, rice, chickpea, maize, faba beans, and mungbean, salinity can inhibit seed germination (Ji *et al*., 2020). This could be because of the osmotic potential i.e., the higher outer side of the seed, which prevents water absorption, or because of the pernicious impacts of Na^+ and Cl^-. For proper growth and development of plants, K^+ ions absorption is necessary but high Na^+ concentrations prevent their absorption. Uptake of salt intervenes with plant's nutritional homeostasis and raises ionic ratios such as Na^+/K^+, Cl-/H_2PO_4, Cl^-/NO^{3-}, Na^+/Mg^{2+} and Na^+/Ca^{2+} which has a negative impact on plant cellular activities (Rane *et al*., 2021). Salinity tolerance varies greatly among crop species and cultivars. At important growth stages including germination and early growth, bread wheat is more tolerant to salinity stress than durum wheat. These discrepancies in reactions are attributable to differences in durum and bread wheat's potential to remove sodium ions (Na^+) from the leaves and distinguish b/w Na^+ and K^+. It affects the growth of plants in cereal crops such as wheat, maize, rice, and chickpea, linseed via imbalances in ions, modifications in oxidative mechanism, metabolic control, nutritional problems, instability of membrane, and reduced rate of differentiation of cells (Yadav *et al* 2024; Sawariya *et al*., 2025). Many facets of biological activities are affected by salt stress, comprising transcription and translational changes. DCL1 - 11 allele (mutant) is more sensitive to salt and other abiotic stressors, involving abscisic acid. Other biogenesis factors including hen1-16 (allele of HEN1), hsty (allele of HASTY), hyl1, and se-1 (allele of SE), also display more sensitivity to salt stress, implying that miRNAs have a function in controlling responses of plants against salt stress. Under salt stress, *Arabidopsis* showed that miR393, miR397, and miR402 were increased, while miR389a.1 was inhibited. In the presence of NaCl, over-expression of transgenic miR417 showed lower seed germination and growth, indicating that miR417 plays a negative function in salinity response. Rice and *Arabidopsis* transgenic lines over expressing osa-miR393 depicted reduced salt and alkali tolerance, showing that miR393 is a positive regulator of salt sensitivity.

Different strategies, particularly those that are effective in controlling water homeostasis and preventing damage, have been adopted to assist plants in better tolerating salt. In order to combat the negative effects of excessive salinity stress, plants developed several sophisticated mechanisms. One such well-known mechanism is stress tolerance, which has been developed from silicon. As was mentioned previously, Si inhibits the intake of harmful ions by depositing Si on the roots, which combats salinity stress. Additionally, silicon reduces osmotic stress brought on by salt by raising the activity of aquaporins, increasing the root hydraulic conductivity.

According to studies, inoculating many plant species with endophytic bacteria can lessen the consequences of salinity stress. For example, when exposed to NaCl, lettuce seeds inoculated with *Azospirillum* displayed improved germination rates and vegetative growth over non-inoculated control plants. According to certain research studies, the significance of lower internal ethylene levels in bacterially mediated resistance to salt stress has been underlined. When compared to strains deficient in the enzyme, the impacts of ACC deaminase-containing *Pseudomonas fluorescens* TDK1 on the growth of groundnut plants were more evident. Maize i.e., salt-stressed inoculating with ACC deaminase carrying *Enterobacter aerogens*, *Pseudomonas syringae*, and *P. Fluorescens* led to greater K^+/Na^+ ratios as well as higher relative water content, chlorophyll, and low levels of proline. ABA is a powerful seed-priming hormone that can promote germination and a crop species' tolerance to a variety of stresses. Rice, wheat, and sorghum grew more after receiving ABA seed priming, improving their ability to withstand salinity (Fig. 4). According to a study, ABA priming increased the development of barley leaves by lowering transpirational water loss in saline environments. The Concentration of Na^+ decreased cellularly and the level of proline increased and sugar build-up in salt-stressed rice leaves were two effects of rice seeds primed with ABA at 10^{-5} M that increased osmoregulation.

The production of glutathione S-transferase-, glutaredoxin-related genes, and peroxiredoxin-genes in the genome of LK11 allowed the bacterial endophyte *Sphingomonas* sp. LK11 greatly improves the shoot/root growth, reducing the stress of salt in wild-type and Got-3 tomato plants (Khan *et al*., 2017). The root endophytic filamentous fungus *Piriformospora indica* was used to inoculate rice plants, and these plants displayed significantly improved root and shoot lengths, fresh& dry weights, and content of photosynthetic pigments. This may be because the enhanced buildup of proin plants increased their capability to tolerate salt stress.

Plants' responses to Heavy metal stress and their mitigation strategies

Heavy metals, naturally occurring elements in the Earth's crust, have become a pressing environmental concern due to human activities and industrial waste. The contamination of soil and water with heavy metals disrupts ecosystems, as these non-biodegradable pollutants persist indefinitely in

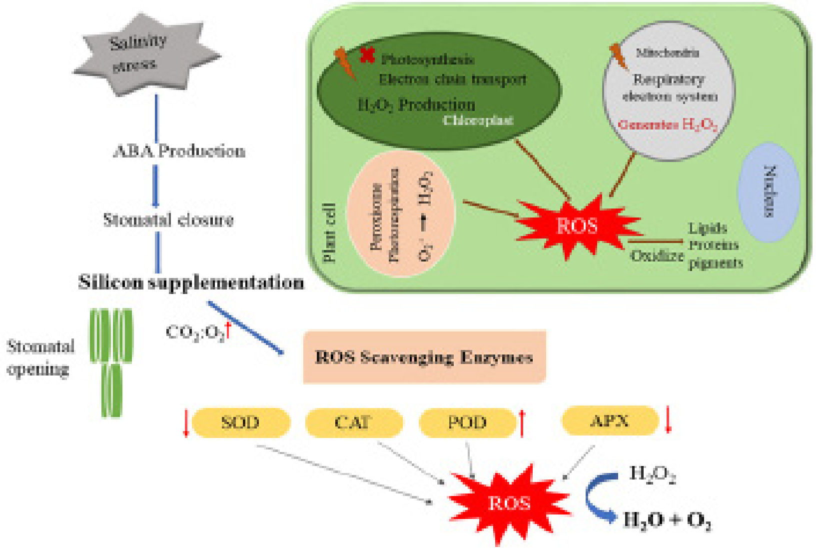

Figure 4: A schematic illustration depicting the generation of ROS and the function of ROS-scavenging enzymes in enhancing silicon-induced salinity tolerance in plants. (Modified from Dhiman *et al.*,2021)

the environment. Their accumulation in plants facilitates entry into the food chain, leading to antagonistic impacts on plant growth and posing health risks to humans and animals. While some heavy metals are crucial in trace amounts for plant growth and metabolic functions, excessive concentrations can disrupt physiological processes and biochemistry. High levels of heavy metals inhibit plant growth, reduce biomass, and impair vital processes like photosynthesis, mineral uptake, and water relations (Li *et al*., 2013). Specifically, toxicity impacts include altered membrane permeability, enzyme inhibition, photosystem damage, and disrupted mineral metabolism. Furthermore, heavy metal exposure leads to oxidative stress, pigment dysfunction, and changes in protein activity. ROS generated under metal stress can destroy cellular organizations through protein and lipid oxidation, nucleic acid damage, and enzyme inhibition (Adrees *et al*., 2015). Heavy metals like copper (Cu) and zinc (Zn) are essential for normal cellular functions but can become toxic at high concentrations. For example, wheat grown on Cu-enriched soil exhibited reduced chlorophyll content, reflecting inhibited enzymatic processes and nutritional imbalances. Such toxicity underscores the need to manage heavy metal contamination to safeguard plant health and overall ecosystem integrity. Chromium (Cr) exhibits toxic impacts on wheat seed germination and seedling growth across various cultivars (HD2932, KO512, DBW14, WH775, and HD2956). Studies show that increasing Cr (VI) concentrations (25–125 ppm) reduces seed germination and escalates plant toxicity, with root growth being most affected. Lead exposure similarly decreases root length and dry mass, causing cell wall damage due to the activation of wall-degrading enzymes. Plants combat heavy metal (HM) stress through intricate defense mechanisms. Physical barriers like thick cuticles, trichomes, cell walls, and mycorrhizal symbiosis act as the first line of defense, with trichomes aiding in metal storage or detoxification (Hauser, 2014). Once metals penetrate, plants deploy cellular strategies such as producing macromolecules like phytochelatins (PCs). Phytochelatins are critical in detoxifying heavy metals and mitigating other stressors like salinity and UV-B radiation. PCs, synthesized in the cytosol and transported to vacuoles as metal-PC complexes, have been used as biomarkers for early HM stress detection. Key genes for PC synthesis, such as AtPCS1 (*Arabidopsis thaliana*) and TaPCS1 (*Triticum aestivum*), highlight their universal significance in plant defense. Roots and aerial organs synthesize and accumulate phytochelatins (PCs), though most studies suggest primary biosynthesis occurs in roots. In sunflowers exposed to cadmium (Cd), root PC levels were twice those in leaves. Similarly, arsenic-PC complexes in rice roots help block arsenic transport to shoots, leaves, and seeds, reducing toxicity in edible parts. Prolonged Cd exposure in *Brassica juncea* (Kumar *et al*., 2024a, 2024b) led to a threefold PC increase in leaves compared to roots, while in corn, prolonged Cd treatment decreased root PC activity but increased phytochelatins synthase levels in leaves, possibly due to feedback regulation or substrate reduction.

Metallothioneins (MTs) are cysteine-rich proteins found in eukaryotes and some prokaryotes. They bind metals like copper, zinc, cadmium, and arsenic, aiding in heavy metal (HM) detoxification, metal homeostasis, and transport regulation. MTs also scavenge reactive oxygen species (ROS), regulate redox levels, repair membranes, and support cell development. Plant MTs are classified into four types, expressed in specific tissues and stages. For instance, OsMT1a in rice helps zinc homeostasis in roots, while MT3 maintains zinc and copper levels in barley seeds. Ectopic expression of MTs in transgenic plants, like OSMT1e in tobacco, enhances metal tolerance (Maheswari and Dubey, 2011). Ferritins, multimeric proteins storing iron and other metals, protect against oxidative damage by scavenging free iron. In plants, ferritin production is triggered by stressors like iron overload and photo inhibition, regulated by ABA and antioxidants. Proline (Pro) accumulates in plants under HM stress, aiding osmoprotection, enzyme stabilization, and growth restoration. Its increase is linked to de novo synthesis or reduced degradation. Proline accumulation helps with osmotic adjustment and protecting macromolecules, particularly under cadmium stress (Maheswari and Dubey, 2011). Antioxidants are vital in alleviating oxidative destruction triggered by ROS in metal-rich environments. In *Triticumaestivum*, lead exposure increased peroxide levels and catalase (CAT) activity, but prolonged exposure reduced peroxidase activity, impeding cellular metabolism (Tripathi *et al*., 2013). Phenolic compounds in plants chelate metals and protect against oxidative stress by stabilizing membranes and preventing ROS damage. Many non-essential hazardous biometals that affect physiology and metabolism are frequently exposed to plants. MeJA can be applied exogenously to plants to reduce their sensitivity to metals. Some studies suggest that MeJA can help reduce the toxic signs caused by boron, arsenic (As), Cd, Cu, Pd, Ni, and Al. External administration of MeJA increases the activity of photosynthetic pigments and photosystem-II in a dose-dependent manner at high concentrations of copper and cadmium.

By boosting the activities of SOD and peroxidase (POD) in seedlings, seed priming with JA in Cu-stressed *Cajanus cajan* promotes the formation of chlorophyll and carotenoid pigments while also neutralizing the negative effects of Cu. Like this, foliar application of JA reduces the build-up of cadmium in different parts of plants, boosts the activities of antioxidants, and reduces the accumulation of osmolytes in faba bean plants, decreasing the deleterious impacts of Cd. Additionally, tomato plants' Pb uptake was decreased by JA, which also increased the ascorbate-glutathione cycle, enhanced photosynthetic properties, metal chelating chemicals, and growth. *Chlorella vulgaris* under Pb stress had much lower H_2O_2 and malondialdehyde levels, which supported the considerable increase in antioxidant capacity (Bali *et al*., 2018) (Table 3).

To reduce stress-related damages, ascorbate can be applied externally to the leaves, and seeds. Numerous studies have examined the modulation of supplementary AsA-mediated antioxidant defense in response to various stresses, comprising salt stress, drought, high temperature, ozone, and heavy metal stress. Plant tolerance to metal stress was also improved by seed priming with AsA. In light of this, the application of AsA to the seeds of *A. esculentus* indicated a reduction in the oxidative stress generated by lead. This was substantiated by a drop in the levels of both peroxidase and malondialdehyde. The surge in endogenous AsA instigated by exogenous AsA promoted the reduction of oxidative stress in Pb-stressed *A. esculentus*, as did the up-regulation of CAT, SOD, and POD activities. In Pb-exposed seedlings, priming of AsA also raised the anthocyanin concentration, which again improved the endurance of metal by reducing ROS generation. Additionally, the AsA supplementation demonstrated its usefulness in reducing oxidative stress caused by Cd. It has been observed that using AsA as a foliar spray could develop into a powerful technique to reduce the toxicity of Cd in *Zea mays* (Zhang *et al*., 2019).

Plants responses to High Irradiance and mitigation strategies

Light is necessary for the growth and development of plants, with its intensity varying dramatically from bright sunlight to complete dark. This range can fluctuate rapidly, such as during sunrises or sunsets, or more gradually over the course of a day. However, both excessively high and low light levels can stress plants, negatively impacting their growth. High light intensity can overwhelm the plant's photosynthetic machinery, causing the formation of harmful oxygen radicals, photo-inhibition, and a reduction in photosynthetic

Table 3: shows the plant's responses to jasmonic acid (JA) under heavy metal stress.

Crop	*Heavy metal stress*	*Response in plants*	*Reference*
Artemisia annua	Boron	MeJA inhibits oxidative stress and controls the production of artemisinin and antioxidant enzymes.	Aftab *et al*. (2011)
Cajanus cajan	Cu stress	JA reduced the toxicity of metals and promoted the accumulation of carotenoids and chlorophyll.	Hanaka *et al*. (2015)
Viciafaba L.	Cd stress	reduced the amount of Cd that accumulated in plant sections while increasing osmolyte accumulation and antioxidant activity	Ahmad *et al*. (2017)
Chlorella vulgaris	Pb stress	JA decreased the amounts of H_2O_2 and malondialdehyde while increasing antioxidant ability.	Ahmad *et al*. 2017
A. thaliana	Al	JA increased the suppression of Al-induced root development.	Yang *et al*. (2017)
Brassica napus	Arsenic	Root growth improved with the treatment of MeJA	Farooq *et al*.(2018)

efficiency. On the other hand, insufficient light limits energy availability, hindering plant growth. To cope with varying light conditions, plants have evolved strategies to regulate light absorption and protect themselves from damage. These include changes in leaf position, structure, reflectance, and the accumulation of inorganic deposits or air-filled hairs. Additionally, plants have developed mechanisms like energy quenching and antioxidant systems to manage excess light energy and scavenge ROS, minimizing photo-oxidative damage and optimizing photosynthesis. Chloroplast movements in response to light intensity are crucial for minimizing photodamage. Under high light, chloroplasts move to the cell's lateral sides, reducing light absorption and preventing excess damage. This movement is regulated by phototropins, with PHOTOTROPIN2 in *Gossypium hirsutum* playing a crucial role in chloroplast avoidance (Shang *et al*., 2019). Excessive light can cause photo inhibition, leading to the inactivation of PSII due to ROS damaging its reaction centers. Restoration of PSII involves the degradation of damaged D1 proteins and the synthesis of new ones (Li *et al*., 2018) (Figure 5). To deal with light stress, plants utilize mechanisms like heat dissipation, cyclic electron flow (CEF), and the xanthophyll cycle (VAZ cycle) to protect against ROS and photoinhibition (Ruban, 2016). High light increases CEF activity and the VAZ cycle, while low light promotes higher PSII quantum yield and faster PSII to PSI electron flux. Plants adapt to light stress both acutely (within hours) and chronically (over days/weeks) to optimize their survival. High-light environments also trigger stronger redox signaling and photorespiration.

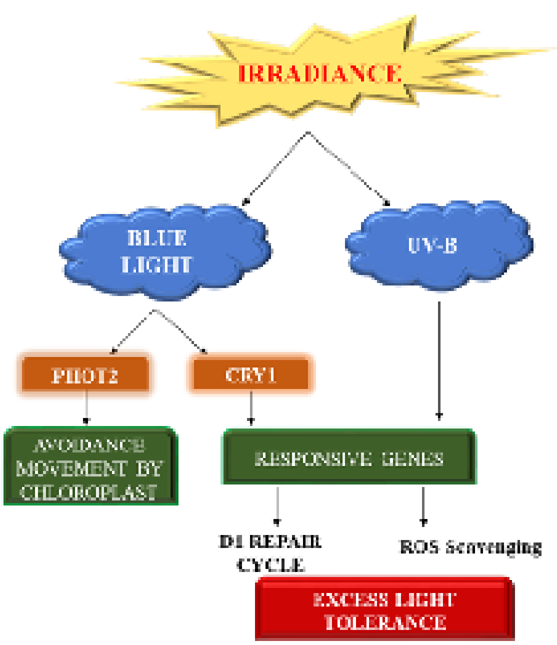

Figure 5: Effects of light stress showing chloroplast avoidance and activation of D1 repair protein and ROS scavenging.

According to a study, the greater activities of DHAR led to the AsA-GSH (Ascorbic acid and glutathione) redox pool's ability to protect Arabidopsis against high-light-mediated oxidative stress. High light (HL) stress, however, was discovered to be caused by both AsA and GSH. After that, it was found that AsA and GSH deficiencies were responsible for the Arabidopsis mutant's vulnerability to HL stress. A mutant of *Arabidopsis thaliana* (vtc2-1) which lacks AsA subjected to high light, observed a high level of H_2O_2 in comparison to the wild type, which was strongly and inversely linked with the total content of AsA. The deficiency of AsA is also responsible for the lower content of chlorophyll, fluorescence characteristics of chlorophyll, and photochemistry of Photosystems - II (PS II). In a recent study, it was observed that *A. thaliana* exposed to HL examined the metabolomics of this plant and discovered that higher GSH biosynthesis backs the photochemistry that aids *Arabidopsis*'s greater survival under HL (Choudhury *et al*., 2018).

Conclusion and future perspectives

Abiotic stresses, such as drought, salinity, heat, and heavy metal etc., pose significant threats to global agricultural productivity. To address these challenges, researchers and practitioners have developed diverse strategies to enhance crop resilience. This review underscores the importance of integrating physiological, molecular, and agronomic approaches to mitigate these stresses effectively.

Physiological strategies, including optimizing water use efficiency and regulating stomatal activity, have proven effective in enhancing plant tolerance to drought conditions. Osmoprotectants like proline, glycine betaine, and trehalose play a crucial role in maintaining cellular stability during stress. Additionally, research on plant signaling pathways, particularly those involving abscisic acid (ABA) and reactive oxygen species (ROS), has shed light on the mechanisms of stress perception and response. Advances in molecular breeding and genetic engineering have led to the development of stress-tolerant crops by identifying and over-expressing key stress-responsive genes such as DREB, HSPs, and aquaporins. Emerging genome-editing technologies have further enabled precise targeting of genes associated with abiotic stress tolerance, overcoming the limitations of traditional breeding methods. Multi-omics approaches, including transcriptomics, proteomics, and metabolomics, have provided deeper insights into stress adaptation, identifying new targets for intervention.

Addressing abiotic stress in agriculture requires a comprehensive and collaborative approach. Integrating multi-omics platforms genomics, transcriptomics, proteomics, and metabolomics—will provide a holistic understanding of plant stress responses and uncover critical regulatory networks for genetic enhancement. Advanced breeding techniques, including genome editing and speed breeding, will be instrumental in creating stress-resilient crops. By combining cutting-edge technologies with sustainable practices, the agricultural sector can build resilience and secure food production amidst a changing climate.

Credit authorship contribution statement

HG: Writing original draft; NY, AK, MJ: Editing and proof reading; SSA: Conceptualization, Supervision & editing; MS, NK, HM, SK, SS, RV: Figure and table editing

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