



International Journal of Research in Agronomy

E-ISSN: 2618-0618

P-ISSN: 2618-060X

© Agronomy

NAAS Rating (2026): 5.20

www.agronomyjournals.com

2026; 9(2): 01-11

Received: 02-09-2025

Accepted: 04-11-2025

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Abiotic stress in field crops: A review

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DOI: <https://www.doi.org/10.33545/2618060X.2026.v9.i2a.4813>

Abstract

The simultaneous occurrence of abiotic stressors, such as heat, drought, salinity and cold, poses a critical threat to global crop productivity. This review evaluates the multifaceted impacts of coupled abiotic challenges on major crops, including wheat, maize and barley. Physiologically, combined stresses disrupt plant homeostasis by impairing photosynthesis, respiration and nitrogen fixation. These challenges lead to leaf withering, reduced biomass and significant reproductive failures, such as pollen sterility and decreased grain weight. At the molecular level, plants initiate complex signaling pathways involving reactive oxygen species (ROS), calcium-permeable channels (CNGCs) and key transcription factors like heat-shock factors (HSFs) and the ICE-CBF-COR pathway. Hormonal regulation, particularly mediated by abscisic acid (ABA), further facilitates long-distance stress signaling and transpiration control. To mitigate these impacts, the review highlights sustainable agronomical practices, including mulching, organic manuring and precise irrigation. Furthermore, future advancements rely on biotechnological approaches such as CRISPR-mediated genome editing, QTL mapping and molecular breeding to develop climate-resilient cultivars. Integrating functional and comparative genomics with sustainable management is essential for ensuring global food security under increasingly frequent environmental extremes.

Keywords: Abiotic stress, heat, drought, salinity, low temperature, combined stress conditions, crop, stress signaling pathways

Introduction

Due to their sessile nature, plants are often exposed to a variety of environmental stressors in field settings. Drought, soil salinity, heat, cold and other abiotic stressors, such as waterlogging and metal toxicity, are significant limiting factors that impact crop yield in both qualitative and quantitative ways (Bashir *et al.*, 2019; Shabbir *et al.*, 2021) ^[51, 107]. Climate change and the demands of an expanding human population are projected to make these challenges much more serious. There are currently 8.2 billion people on the planet and according to the United Nations' most recent estimates, that number might rise to 8.5 billion by 2030 and 9.7 billion by 2050 (United Nations, 2024) ^[125]. Therefore, a major obstacle to agriculture's efforts to fulfill the world's expanding food demand is environmental change. Regrettably, stressful situations are present in the great majority of land (Cramer *et al.*, 2011) ^[37]. Abiotic stress can lower yields by over 60% on average when compared to record yields (Boyer, 1982) ^[48]. Plant growth and development processes are severely impacted when these stresses occur at any stage of development (Javed *et al.*, 2020) ^[121]. Under field conditions, salinity and drought (Paul *et al.*, 2019) ^[56]. Salinity and waterlogging (Mahmood *et al.*, 2021; Hussain *et al.*, 2022) ^[124, 114] and temperature and drought stresses (Nasser *et al.*, 2020) ^[64] often coexist. Crop performance is at risk when these pressures coexist (Duan *et al.*, 2018) ^[39]. Globally, temperature variability patterns show that heat extremes are becoming more common than cold ones and climate extremes show an increasing poleward gradient (Zhang *et al.*, 2022) ^[145]. According to a recent study using a machine learning algorithm and sub-national yield data, climate extremes could account for as much as half of the variability in agricultural yields worldwide (Vogel *et al.*, 2019) ^[32]. Osmotic stress is caused by salt-alkalization and water deficiency stressors that interfere with ionic equilibrium and plant homeostasis (Shahid *et al.*, 2022) ^[118]. Salinity significantly raises the amounts of Na⁺ and Cl⁻ in leaves during drought stress, which can

seriously impair seedling growth (Shahid *et al.*, 2022) ^[118]. Excessive soil salinization and wet conditions, which are frequently indistinguishable, are increased when salinity and drought pressures coexist. When salinity stress and waterlogging stress coexist, it can seriously harm agricultural plants and have a significant effect on yield (Mahmood *et al.*, 2021) ^[124]. The main sources of coupled salinity and waterlogging stress are intensified saline water tables and intensive irrigation techniques (Wichelns and Qadir, 2015) ^[27]. Temperature stress and the concurrent occurrence of drought, which is caused by an uneven distribution of rainfall, have raised leaf temperatures and caused plants to lose water quickly (Lawas *et al.*, 2018) ^[63]. Crop shows symptoms of having these stresses later on after their physiology undergoes significant changes (Cramer *et al.*, 2010) ^[35]. According to the study, yield anomalies are more closely linked to temperature-related extremes than precipitation-related parameters when regular irrigation is in place. During drought stress, high temperatures led to a higher reduction in net CO₂ diffusion and nutrient uptake, which decreased photosynthesis (Lamaoui *et al.*, 2018) ^[79]. The morpho-physiological and molecular strategies used by plants to deal with the simultaneous occurrence of various abiotic challenges are quite similar (Mahmood *et al.*, 2021; Hussain *et al.*, 2022) ^[124, 114].

Where crops are best grown depends on the conditions they need to grow at their best and reach marketable quality (Li *et al.*, 2023) ^[24]. Some of the most widely grown crops in the world are wheat, rice, sugarcane, maize (*Zea mays*), potatoes, barley, sunflowers (*Helianthus annuus*), rapeseed (*Brassica napus*) and tomatoes. One of the primary crops grown in the world and around the world is wheat. Although it can withstand a wide variety of temperatures and environmental conditions, high heat and severe rainfall can spread common illnesses that reduce production (Song *et al.*, 2019) ^[143]. Wheat growth and development are further hampered by high soil salinity and water scarcity (Abbas *et al.*, 2013; Zhang *et al.*, 2018) ^[3, 130]. Due to its high water requirements, maize is another significant cereal that is vulnerable to drought, especially during crucial growth stages like the seedling or reproductive stage (Zhang *et al.*, 2018) ^[130]. Several processes assist it in controlling the distribution of salt and other solutes within its tissues and maintaining its water content. On the other hand, potatoes are among the most drought-sensitive crops (Obidiegwu *et al.*, 2015; Dahal *et al.*, 2019) ^[46, 52]. Barley has a great degree of resilience to abiotic stress and is arguably the most salt-tolerant cereal (Munns and Tester, 2008) ^[103]. However, in conditions of drought and salt stress, their growth and output are still restricted (di Caterina *et al.*, 2007; Keipp *et al.*, 2020) ^[97, 53]. Although tomatoes may be grown in nearly every climate on the planet, dryness, high salinity and extreme temperatures have an impact on their yield (Zhou *et al.*, 2017; Zhou *et al.*, 2019; Alam *et al.*, 2021) ^[108, 109, 83]. Abiotic factors that impact crop plants include heat, cold, salinity and drought.

An astounding amount of research has been documented on the individual occurrence of environmental stresses and their independent response in plants, despite the increasing prevalence of coupled abiotic challenges in field settings (Hu *et al.*, 2015; Shahzad *et al.*, 2021) ^[133, 58]. In order to assess the effects of coupled abiotic challenges on plant performance as well as the adaptive mechanisms in plants, especially at the physiological and molecular levels, the current review-based study was conducted.

Abiotic Stresses and Crops

Heat Stress

Effects of heat on crop yield

The type of crop, cultivar and growth stage all affect the optimal temperature (Manivannan and Jaleel, 2007) ^[90]. High temperatures led to poor wheat crop seed yield and physical characteristics (Grass and Burris, 1995; Joshi *et al.* 2016) ^[62, 77]. said that damage from high temperatures throughout grain developing phases is the source of grain weight losses. High temperatures in the field before and during anthesis cause grain weight loss, according to research by Calderini *et al.* (1999) ^[23] and Wardlaw (2002) ^[45]. According to Kamal *et al.* (2017) ^[69], heat stress increases thermosensitivity by preventing the formation of phenolics, proline and other secondary metabolites. According to Kousar *et al.* (2018) ^[100], heat stress lowers plant output because it negatively affects grain growth, including assimilate translocation, length and rate of grain filling.

Role of High Temperatures in Crop Production

Exposure to temperatures over the ideal range that are high enough to permanently harm a plant's growth and development is known as heat stress (Kotak *et al.*, 2007) ^[116]. Plant vegetative phases, resource allocation and, most importantly, reproductive activities are all directly impacted by higher temperatures, which can result in a significant decrease in yields (Khan *et al.*, 2022) ^[9]. Rapid cellular damage and death are caused by extremely high temperatures (Locato and de Gara, 2018) ^[126]. In the vegetative stage of a plant's growth, heat stress can cause a decrease in photosynthesis, which can then result in a decrease in biomass (Liu *et al.*, 2016) ^[15]. The reproductive stages of development are greatly impacted by higher temperatures. Temperatures above 29.5 °C reduce flowers, pod numbers, seed weight and overall yield for Brassica species from bolting to the end of flowering (Morrison and Stewart, 2002) ^[76].

Heat exposure during spring wheat gametogenesis is a significant determinant of yield loss, according to (Aiqing *et al.*, 2018) ^[111]. After applying heat stress to spring wheat genotypes, Bheemanahalli *et al.*, 2019) ^[96] found a 2-93% decrease in pollen germination. Kernel abortion, which can be caused by the inadequate utilization of soluble sugar due to the regulation of starch synthesis during heat and drought stress, typically reduces maize output (Liu *et al.*, 2020) ^[135]. The negative impact of heat stress on pollen viability was also highlighted by these scientists. Grain weight decreased by 28% in maize due to high temperatures during the entire grain-filling stage (Wang *et al.*, 2021) ^[136]. Crop plants are particularly vulnerable to heat stress during reproductive stages, as numerous authors have demonstrated.

High-Temperature Signaling in Model Plant and Crops

In response to heat stress, a number of thermosensors and thermosensitive components have been described. Thermosensors are components that satisfy three requirements: a direct interaction with heat-stress conditions causes a change in their structure or activity; this change results in significant signals or responses; and these processes result in physiological and morphological changes or stress responses (Lamers *et al.*, 2020) ^[47]. Changes in protein structure and membrane fluidity can be assessed as thermosensors under these circumstances (Vu *et al.*, 2019) ^[61]. High temperature-induced changes in membrane fluidity cause Ca²⁺ influx because they activate Ca²⁺-permeable channels that are members of the CYCLIC NUCLEOTIDE-GATED CHANNEL (CNGC) family (Saidi *et*

et al., 2009) ^[142]. In *Oryza sativa*, some CNGCs have been demonstrated to induce thermotolerance (Cui *et al.*, 2020) ^[138]. Downstream elements that are more accurately described as thermoresponsive follow the reversal of phytochrome (Vu *et al.*, 2019) ^[61]. The phytochrome-interacting factor (PIF) family is the most well-known class of thermos-responsive interacting partners (Pham *et al.*, 2018) ^[128]. In maize, the significance of elevated PIF expression levels under high temperatures has been verified (Gao *et al.*, 2019) ^[140]. Reactive oxygen species (ROS), transcription factors and protein kinases are additional crucial signaling components (Qu *et al.*, 2013) ^[14]. A class of active transcription factors known as heat-shock factors, or HSFs, can induce the production of many heat-shock proteins. The alternative splicing mechanism has been confirmed as a novel component of heat-shock memory in wheat, barley, rice and maize (Cheng *et al.*, 2014; Ma *et al.*, 2023) ^[94, 148].

Drought Stress

Effects of drought stress on crop yield

According to Mafakheri *et al.* (2010) ^[2], yield was considerably decreased during drought stress as a result of decreased pod count in the plants. According to Boyer (1971) ^[49], one of the main problems with crop yield, plant health and overall productivity is water scarcity. Drought stress is a complicated condition influenced by edaphic and other climatic changes, according to Serraj *et al.* (2003) ^[106]. Drought stress during vegetative phases decreases the rice crop's developmental progress, according to Manikavelu *et al.* (2006) ^[10]. According to Harris *et al.* (2002) ^[21], dryness primarily hindered germination and encouraged poor stand establishment. According to Serraj *et al.* (2005) ^[105], yield losses may result from intermittent drought throughout the vegetative process, drought during reproductive growth, or drought at the end of the crop cycle. In a study on maize using six treatments with various irrigations, Khan *et al.* (2001) ^[70] found that when water stress rose, plant height, stem diameter and leaf areas significantly decreased.

High Temperatures without Precipitation Are Causing Drought

Drought stress is closely linked to high temperatures. A drought occurs when there is either insufficient or no rain for an extended period of time, leading to a significant hydrological imbalance. Due to their sessile nature, plants are directly impacted by drought stress due to a lack of water. Water availability is declining and demand is rising, making drought stress more severe. 70% of the world's clean water needs are currently met by agriculture and this proportion is predicted to rise quickly in the years to come (Boretti and Rosa, 2019) ^[5].

Impact of Drought on Different Crops at Different Developmental Stages

The degree of drought stress determines how drought affects yield. As has been demonstrated for barley in field settings, severe drought can kill plants, resulting in a complete loss of production without irrigation (Samarah *et al.*, 2009) ^[86]. According to a meta-analysis based on field experiment data, yield loss when water was cut by about 40% ranged from about 21% in wheat to 39% in maize (Daryanto *et al.*, 2016) ^[112]. Drought is expected to reduce wheat and maize yields by 10% in European countries (Webber *et al.*, 2018) ^[43]. Similar to other abiotic stresses, drought-induced yield loss differs among cultivars (Samarah *et al.*, 2009; Mickky *et al.*, 2020) ^[86, 16] and this is an important consideration when comparing species in

terms of drought resistance.

Additionally, dryness degrades crop quality; for example, rapeseed seeds under water scarcity have been found to have a reduced seed oil content (Hussain *et al.*, 2018) ^[74]. The stage of plant development when impacted by drought is another important determinant in yield loss. Better timing of plant growth could increase yields since plants exposed to stress during the reproductive stage are more susceptible to drought (Daryanto *et al.*, 2016; Wiegmann *et al.*, 2019) ^[112, 85]. Grain filling, flower production, seed composition and longevity are all reduced by extended exposure to drought stress throughout the reproductive phase (Farooq *et al.*, 2016) ^[73].

Drought in Plant Physiology

The primary issue with drought is the start of numerous interconnected positive feedback loops that worsen drought-stress conditions and limit above-ground development. One such restriction is the stomata's closure as a defense against water loss, which lowers the content of CO₂. In turn, ROS damages the photosynthetic machinery and oxidizes other crucial molecules, such as lipids and proteins. In C3 plants, the transpiration ratio for CO₂ fixation is approximately 400 (Taiz *et al.*, 2015) ^[67]. However, there are significant disadvantages to limiting CO₂ levels and the necessity of preserving adequate CO₂ levels has caused light responses and CO₂ uptake in CAM plants to evolve apart.

The beginning of leaf-tissue warming is another characteristic of stomata closure. Reduced photosynthetically active area results from a drop in plant growth, leaf area and number due to a reduction in nutrient acquisition and a loss of turgor caused by a decrease in water mass flow (Raza *et al.*, 2023; Farooq *et al.*, 2009) ^[12, 71]. Instead of allocating their resources to the best possible growth, plants are compelled to produce osmoprotective chemicals. In general, a variety of physiological processes are impacted by drought stress, which eventually results in growth limitations and reduced output (Parihar *et al.*, 2015; Munns and Tester, 2008) ^[91, 103].

The Role of Root Growth in Drought Resistance

Improving water absorption, lowering water loss and enduring water deprivation are the primary counteracting processes, albeit the response to drought stress varies depending on its intensity (Li *et al.*, 2021) ^[44]. Efficient root growth is the primary driver of water uptake. It's interesting to note that earlier breeding techniques were primarily concerned with above-ground organs, ignoring root systems or only implicitly or indirectly gaining their characteristics (Siddiqui *et al.*, 2021) ^[80]. Therefore, a prospective source of genetic variety for stress adaptation is the roots and their flexibility. Several teams have discovered QTL that affect physiological and root characteristics in significant crops throughout the past ten years (Siddiqui *et al.*, 2021) ^[80]. The root system's deep, branching rooting and effective water uptake are generally advantageous in drought circumstances. In the current field circumstances, plants with shallow roots, such as the Styrian pumpkin (*Cucurbita pepo* L. *Styriaca*), may have significant issues absorbing water (Dietz *et al.*, 2021) ^[59] (Dietz *et al.*, 2021) ^[59]. In this regard, describing the DEEPER ROOTING 1 (OsDRO1) gene in rice has shown the significance of root growth angle (Uga *et al.*, 2013) ^[144].

In drought conditions, OsDRO1 maintains a high yield and encourages deep rooting. It has recently been demonstrated that the analogous gene ZmDRO1 in maize modulates root angle and increased expression of this gene after stress signals has been linked to increased yields under field circumstances (Feng *et al.*,

2022)^[131]. However, as has been demonstrated for maize (Feng *et al.*, 2022)^[131], DRO1 ectopic expression without a stress signal may have detrimental effects even in non-stressed settings. Arabidopsis that expresses the potato StDRO1 gene has also shown the beneficial impact of root architecture on drought tolerance (Sun *et al.*, 2022)^[18]. According to these results, root architecture-focused breeding and the identification of these genes in other crops like wheat and barley (Ashraf *et al.*, 2019)^[4] may be effective ways to maintain yields under drought.

Roots and Hydrotropism

Growth toward areas of the soil with higher water potential may be important in water-limiting settings because water is not evenly distributed throughout the soil. Root hydrotropism in the model plant Arabidopsis has been demonstrated to be significantly influenced by the signaling pathway using the Ca²⁺ channel pattern along root cells, endoplasmic reticulum-localized type 2A Ca²⁺-ATPase (ECA1) and MIZU-KUSSEY1 (MIZ1; Shkolnik *et al.*, 2018)^[25]. However, the full molecular mechanism, including the sensor, is still unknown. The function of plasma membrane-localized OSCA1.1 in hydrotropism and root bending has also been verified recently (Akita and Miyazawa, 2022)^[50]. OsOSCA1.2 hyperosmolality gating has been investigated using cryogenic electron microscopy as a prospective candidate for drought resistance and OSCA gene characterization has also been carried out for barley, soybeans and maize (Liu *et al.*, 2022; Cao *et al.*, 2020)^[17, 60].

Long-Distance Signaling of Water Deficit

The primary mechanism for lowering water loss is transpiration regulation. The root-derived short peptide CLAVATA3/ESR (CLE)-RELATED PROTEIN 25 (CLE25) is a component of long-distance signaling. When dryness strikes, CLE25 travels from the roots to the leaves, where it is detected by BARELY ANY MERISTEM (BAM) receptors and causes ABA to build up by triggering the biosynthetic enzyme NINE-CISEPOXYCAROTENOID DIOXYGENASE 3 (NCED3; Takahashi *et al.*, 2018). Research on crop plants has shown that ABA is an essential stress-related phytohormone (Yuan *et al.*, 2019; Li *et al.*, 2019)^[129, 147]. Section 4.2 on metabolites discusses the function of ABA and how it interacts with other plant hormones. ROS also mediates the signal for stomata closure. Stress causes H₂O₂ to activate the receptor LEUCINE-RICH REPEAT RECEPTOR PROTEIN KINASE.

Other Mechanisms of Drought Resistance

By building up osmoprotectants, modifying metabolism, boosting water-use efficiency (WUE) and lessening the impact of the secondary effects of drought, such as enhancing antioxidant metabolism and safeguarding photosynthesis, tolerance to drought is based on compensating for the drop in water potential. In a different section, the function of metabolites in stress tolerance is covered in greater detail.

Salt Stress

Effects of salinity on crop yield

Salinity is one of the most important abiotic stressors affecting plant growth and productivity, particularly in arid and semi-arid regions. The presence of soluble salts in excess amounts in soil affected the plants normal physiological processes and impaired plant growth during salt stress (Cramer, 1997)^[36]. Salinity interrupts germination by reducing the osmotic potential of the soil in which the seed reduces the water. Ditommaso (2004)^[6] noted that plant germination is drastically declining as salinity

stress increases. According to research by Carpici *et al.* (2009)^[149], salt stress is the cause of maize's decreased germination index. According to Ishitani *et al.* (1996)^[75], a high salt level in barley reduced growth and production by 65%. According to Ahmad *et al.* (2002)^[110], salt stress considerably decreased the yield of cotton seeds and dry matter. According to Rengasamy (2006)^[92], the buildup of soluble salts in the soil column seriously harms both agricultural output and the environment. According to, plants close their stomata in an effort to prevent or avoid stress, which causes wilting, stunted development and decreased output.

Food production must increase by 50% by 2050 in order to fulfill the growing demands of an expanding population. Global demands are being limited by a number of issues, chief among them the physical and chemical degradation of soil brought on by salt and erosion. concluded that salinity decreased plant height, the number of leaves on the main stem, the number of branches on the plant, root length, root dry weight and shoot dry weight. According to Pannuccio *et al.* (2014)^[82], the presence of salinity caused a considerable reduction in both shoot and root length. Increased salinity in irrigation water significantly reduced sorghum output and yield components, according to Shakeri *et al.* (2017)^[31]. Tavousi *et al.* (2015)^[84] came to the conclusion that while salinity stress does not influence production, we do observe a decline in yield as salinity grows. As the salinity of the water increases, so does its quality of usage. High salinity conditions result in osmotic stress, which can negatively impact the growth of numerous plants due to challenges in drawing water from the soil and ion toxicity (Al-Taey and Majid, 2018)^[22].

Plants Are Variable in Their Resistance to Salt

As glycophytes, the majority of crop plants are susceptible to salinity stress. According to estimates, salinity affects almost half of all irrigated land (Gong *et al.*, 2020)^[146]. Both human activity (land clearing, irrigation) and natural processes (weathering, rain with sea-salt content) can produce extremely saline soil (Parihar *et al.*, 2015)^[91]. The electrical conductivity of a saturated soil or irrigation water extract is typically used to determine the salinity level. Vegetables that are sensitive to salt, like beans (*Phaseolus vulgaris*), carrots (*Daucus carota*), or onions (*Allium cepa*), can only withstand low salinity levels; their threshold of negative impacts is approximately 1 dS/m, which is far lower than the 4 dS/m criterion used to categorize soils as saline (Munns and Tester, 2008)^[103].

As has recently been shown in laboratory settings for olives (*Olea europaea*; Regni *et al.*, 2019)^[66] and maize (Chen *et al.*, 2019)^[33] and in field settings for wheat, barley (Setter *et al.*, 2016)^[123] and potatoes (Straten *et al.*, 2021)^[38], the yield of a crop produced in soils of increasing salinity varies not only with plant species but also with cultivars. Finding resistant cultivars or types is therefore a viable approach to sustaining yields in areas where the land's salinity is rising, but it is obviously not a permanent solution.

Key Mechanism for Salt-Stress Resistance

Plant growth, development and productivity are all adversely affected by salt stress (Chourasia *et al.*, 2021)^[54]. Two different biophysical effects of elevated salt levels are the production of osmotic stress and the buildup of ions to cytotoxic levels. The second of these outcomes is the subject of this section. Since the homeostatic balance between ion ratios is believed to be the fundamental mechanism of tolerance to elevated salt levels (Assaha *et al.*, 2017)^[26], one of the main effects of excess salt is

ion imbalance within the cell (Guo *et al.*, 2020) ^[95]. A key mechanism for salt tolerance in plants is the Salt Overly Sensitive (SOS) pathway (Ma *et al.*, 2022) ^[65]. The calcium sensors stimulate SOS2 activity by detecting the salt-induced $[Ca^{2+}]_{cyt}$. To phosphorylate the AtSOS1 antiporter and prevent the buildup of Na^+ at hazardous levels, activated SOS2 is recruited to the plasma membrane.

Temperature Stress

Effects of temperature on crop yield

According to Ruelland *et al.* (2009) ^[29], cold stress affects winter wheat and is a limiting factor for crop growth. According to Yoshida (1981) ^[120], plants suffer significant freezing injury issues throughout the early seedling and germination stages. According to Nahar *et al.* (2012) ^[55], cold stress increases early maturity, stunted growth, bushy plants and yellowing of leaves. She also noted that chilling injury in plants decreases plant growth, seed coloration, wheat bands and specks, leaf whitening and fewer tillers. According to Yadav S. (2010) ^[115], low temperature stress impacts plant reproductive stages, resulting in sterile pollen and delayed flowering, which significantly decreases agricultural output. According to Atayee *et al.* (2020) ^[11], cold stress can produce a variety of physiological disturbances in chilling-sensitive plants, which can lead to chilling injury and mortality of many horticultural plants. In reaction to cold stress, proline, a well-known osmo-protectant, builds up. Additionally, it affects almost every facet of cellular activity in plants. One of the most important consequences of dehydration brought on by cold stress is membrane breakdown (Saito K. and Matsuda F. Y, 2010) ^[57]. According to, heat stress during the anthesis and grain filling period hastened early maturity, decreased grain sizes, increased yield losses and caused early senescence and shorter durations of photosynthetic activity.

Crop Sensitivity to Low Temperatures

Regarding their ability to withstand cold, crops can be categorized as freezing-tolerant, chilling-sensitive, or chilling-tolerant (Mahfoozi, 2001) ^[117]. Crop species, cultivars and the developmental stage of a particular plant all affect how sensitive a plant is to temperature thresholds (Mahfoozi, 2001; Li *et al.*, 2015) ^[117, 134]. Many significant crops are capable of developing cold tolerance, but the process of acclimatization is hampered by abrupt temperature changes, which are becoming more frequent due to climate change. The plants may be exposed to unexpected freezing temperatures that they cannot withstand due to the lack of low-temperature-induced cold-hardening brought on by the mild weather that is common in the fall and winter and the decreased snow cover. Low temperatures can nevertheless affect a plant's vegetative and reproductive growth if they are not fatal. Poor germination, chlorosis, wilting, growth retardation, flower abscission, pollen sterility, or decreased fruit set are all consequences of cold stress (Thakur *et al.*, 2010; Borjas *et al.*, 2016; Moradtalab *et al.*, 2018) ^[93, 8, 87]. Low temperatures have an impact on plant and seed quality in addition to total production. In chickpeas (*Cicer arietinum*), cold has been shown to significantly reduce seed size (24%), starch (34%), protein (33%) and fat (43%) reserves while increasing the amount of soluble carbohydrates (Nayyar *et al.*, 2005) ^[41]. Low temperatures lower the amounts of amylose, amylopectin and total starch in wheat grains; nevertheless, more significant alterations have been noted when low-temperature treatments take place during the booting stage as opposed to the jointing stage (Zhang *et al.*, 2021) ^[19]. While maize is seen as a crop that

is vulnerable to cold, potatoes are thought to be a crop that can withstand cold (Rodríguez *et al.*, 2014) ^[127].

Low-Temperature Signaling

Similar to the heat-stress-sensing pathway, these modifications set off a series of Ca^{2+} and MAPK signals (Guo *et al.*, 2018) ^[132]. In rice, COLD1 and Rice G-PROTEIN α SUBUNIT1 (OsRGA1, not to be confused with Following exposure to heat or cold stress, rice cngc14 and cngc16 mutants show decreased survival rates and increased hydrogen peroxide buildup, suggesting a crucial role for CNGC genes in both situations (Cui *et al.*, 2020) ^[138]. The ICE-CBF-COR signaling pathway, which includes an INDUCER OF CBF, is initiated when low temperatures are perceived. ICE1's post-translational modification by HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1 (HOS1) is necessary for its activity (Dong *et al.*, 2006) ^[20]. In addition to directly controlling CBF expression in maize, ICE1 also modifies amino acid metabolism, which in turn controls mitochondrial oxidative bursts that reduce cold tolerance (Jiang *et al.*, 2022) ^[40]. The overexpression of TaCBF14 and TaCBF15 from winter wheat in spring barley, where the transgenes increased the barley's resistance to frost by many degrees, has shown how these genes are involved in the cold acclimation process (Soltész *et al.*, 2013) ^[13].

Role of Redox Changes in Cold Signaling

Cold-mediated redox alterations that cause structural switching and functional activation of CBFs are another way by which temperatures control CBF activity. THIOREDOXIN H2 (Trx-h2), which is myristoylated and attached to cytoplasmic endomembranes, is released during exposure to cold and moves to the nucleus, where it interacts with CBF1. To control downstream targets, Trx-h2 lowers the oxidized CBF proteins and transforms them into an active state (Lee *et al.*, 2021) ^[30].

Combined abiotic stresses: Field reality and impacts Growth and Development Implications of Combined Abiotic Stresses

Plants aFinalre negatively impacted by drought stress at every step of growth and development, from the molecular to the morphological levels (Islam *et al.*, 2021) ^[81]. Salt and other abiotic stresses affect plant roots by raising osmotic pressure outside the roots (Yadav *et al.*, 2020) ^[119]. When water intake and accumulation into developing cells are decreased, enzymatic changes in the cell wall contribute to the suppression of plant development (Javed *et al.*, 2022) ^[122]. Reduced photosynthesis and respiration are the main ways that water scarcity limits plant growth. All cellular processes were interrupted by cold stress, which also reduced electrolyte leakage, plasmolysis and protoplasmic streaming, all of which alternately damaged the cells (Yadav *et al.*, 2020) ^[119]. Along with osmotic stress, salinity causes ionic toxicity, which is associated with oxidative damage and nutritional constraints. Because of osmotic stress and ionic toxicity, high salt concentrations impede plant growth and development (Singhal *et al.*, 2022) ^[99]. Under salt stress, soil osmotic pressure surpassed plant cell membranes, restricting plant uptake of nutrients like K^+ and Ca^{2+} and harming cell membranes and growth. Because of increased osmotic potential and ion toxicity, high soil salinity hinders plant growth and development phases in addition to preventing seed germination (Javed *et al.*, 2020) ^[121].

Physiological Consequences of Combined Abiotic Stresses

Crop productivity losses are caused by a number of

physiological processes that are impacted by coupled abiotic stresses, including photosynthesis, respiration, starch metabolism and nitrogen fixation (Farooq *et al.*, 2015) ^[72]. Physiological alterations include increasing relative stress damage in plants, lowering the osmotic potential, water potential and relative water content of leaves and causing nutritional imbalances. Leaf withering, leaf abscission, a reduction in leaf area and a decrease in water transpiration are further physiological responses to stress (Fghire *et al.*, 2015) ^[98]. Turgor pressure, a crucial physiological process influencing cell development, is lowered by drought stress (Yadav *et al.*, 2020) ^[119]. Additionally, among other effects, drought stress results in longer cells, poor mitosis and shorter plants (Islam *et al.*, 2021) ^[81]. In response to drought, plants mobilize metabolites to change their osmotic balance and produce protective compounds (Gull *et al.*, 2019) ^[7]. By preserving cell water homeostasis, osmotic adjustment can lessen the negative effects of stress (Fghire *et al.*, 2015) ^[98]. When cells and tissues dehydrate and crystallize as a result of cold stress, which results in water stress and electrolyte leakage, decreased membrane conductivity and increased water viscosity, plant growth and development are inhibited (Bahar *et al.*, 2021) ^[1]. Before it hinders development, a lack of water prevents respiration and photosynthesis. Newly split cells around the xylem restrict plant development zones due to their fundamental nature. Both high temperatures and irreversible drought stress, which can kill plants, have an effect on plant growth and development (Hussain *et al.*, 2019) ^[113]. During the reproductive growth cycle, heat stress results in a dysplastic anther by causing cells to lose their ability to function (Gull *et al.*, 2019) ^[7].

Molecular Consequences of Combined Abiotic Stresses

When a plant responds to abiotic stressors, numerous molecular pathways interact and communicate with one another. Many abiotic stress responses are influenced by reactive nitrogen species (RNS) and reactive oxygen species (ROS), which have an impact on gene expression and enzyme activity (Mittler *et al.*, 2011) ^[102]. Cells produce stress proteins, activate antioxidant enzymes, increase the expression of genes involved in antioxidant functions and accumulate suitable materials in response to reactive oxygen species (ROS) (Lu and Zhu, 2017) ^[141]. Certain detoxifying genes, such as ascorbate peroxidase, glutathione peroxidase and glutathione reductase, can help lessen abiotic stress. Hormones like ethylene and abscisic acid can also control plant responses to abiotic stress (Taxak *et al.*, 2017) ^[89].

Agronomical practices towards abiotic stress

By using sustainable agronomic practices and a greater understanding of how crops respond to drought, salinity and cold and heat stressors, abiotic stress can be decreased. By using management techniques like mulching, plant geometry, seed-resistant variety, sowing time and sufficient irrigation, the aforementioned stressors can be sustained without endangering the ecosystem. Pulse crops benefit from deep plowing because it improves root multiplication and increases productivity in shallow areas. Adding organic manure and soil organic matter improves the soil's capacity to store water, which is beneficial for crop water availability. Mulching with plastic or biodegradable films can help minimize water loss through evaporation. Applications of micronutrients during heat stress can increase the potential to conserve water potential in tissues by enhancing heat stress tolerance. According to, the use of antitranspirants improves resistance to drought stress and lowers

transpirational losses and water consumption.

Conclusion and Future Outlook

Global food security is seriously threatened by the simultaneous convergence of abiotic stressors such as heat, drought, salinity and cold. These stresses frequently result in significant yield reductions, sometimes surpassing 50-60%. This analysis assesses the complicated effects of these coupled difficulties on important crops, such as wheat, maize and barley, pointing out that single-stress studies are unable to forecast the intricate interactions between combined stresses. By hindering photosynthesis, respiration and nitrogen fixation, these interactions physiologically upset plant homeostasis. Leaf senescence, decreased biomass and serious reproductive failures, such as pollen sterility and poor grain filling, are examples of such disturbances. At the molecular level, plants start coordinated defensive networks that include important transcriptional modules like the ICE-CBF-COR pathway, calcium-permeable channels (CNGCs) and reactive oxygen species (ROS) signaling. New and species-specific defense mechanisms may be discovered by genome-wide association studies and other modern statistical methods (Kameniarová *et al.*, 2022) ^[78]. Future resilience depends on understudied characteristics like root architecture and hydrotropism to maximize nutrient uptake, but breeding has historically concentrated on above-ground qualities.

This review identifies two strategies to lessen these effects: the immediate use of climate-smart agronomy practices, like mulching and precision irrigation, along with long-term biotechnology developments. QTL mapping will be crucial for creating the next generation of multi-stress-tolerant crops by utilizing CRISPR-mediated genome editing. In the end, ensuring agricultural output in the current era of growing climate uncertainty requires a greater comprehension of how plants integrate various environmental signals. Translating laboratory-defined stress networks into steady field performance in realistic multi-stress situations still has significant gaps, nevertheless.

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