



Review

The Adaptation and Tolerance of Major Cereals and Legumes to Important Abiotic Stresses

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Abstract: Abiotic stresses, including drought, extreme temperatures, salinity, and waterlogging, are the major constraints in crop production. These abiotic stresses are likely to be amplified by climate change with varying temporal and spatial dimensions across the globe. The knowledge about the effects of abiotic stressors on major cereal and legume crops is essential for effective management in unfavorable agro-ecologies. These crops are critical components of cropping systems and the daily diets of millions across the globe. Major cereals like rice, wheat, and maize are highly vulnerable to abiotic stresses, while many grain legumes are grown in abiotic stress-prone areas. Despite extensive investigations, abiotic stress tolerance in crop plants is not fully understood. Current insights into the abiotic stress responses of plants have shown the potential to improve crop tolerance to abiotic stresses. Studies aimed at stress tolerance mechanisms have resulted in the elucidation of traits associated with tolerance in plants, in addition to the molecular control of stress-responsive genes. Some of these studies have paved the way for new opportunities to address the molecular basis of stress responses in plants and identify novel traits and associated genes for the genetic improvement of crop plants. The present review examines the responses of crops under abiotic stresses in terms of changes in morphology, physiology, and biochemistry, focusing on major cereals and legume crops. It also explores emerging opportunities to accelerate our efforts to identify desired traits and genes associated with stress tolerance.



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1. Introduction

Major abiotic stresses that are likely to be amplified by climate change and can destabilize crop yields include drought, extreme temperatures, flooding, waterlogging, soil salinity, acidity, mineral toxicity, and nutrient deficiency. Global climate change and environmental degradation are intensifying the severity of abiotic stresses that adversely affect the growth, development, and productivity of crop plants. The increasing frequency of extreme weather events due to climate change is expected to cause severe risks to sustainable crop production for major cereal and leguminous crop species. Losses in production caused by abiotic stresses may exceed 40% [1], and hence these stresses could be a constant threat to global food security if not properly managed. The Food and Agricultural Organization (FAO) has emphasized that about a 60% enhancement in food production is needed by 2050 to feed a population of about 9.3 billion. This must be achieved with no adverse effects on the environment, which is threatened by the continuous exploitation of natural resources and the loss of biodiversity. In order to ensure sustainability even under the changing climate, it is essential to develop resilient cultivars of crops and suitable crop production practices with insights on stress tolerance mechanisms and the associated traits.

The climate resilience of agriculture depends on crop tolerance to multiple abiotic stresses that cause considerable yield losses individually, as well as in combination. Abiotic stresses negatively impact plant growth, development, reproduction, and ultimately crop productivity. Crops can tolerate certain environmental stresses through their innate adaptation mechanisms, which are driven by various physiological and metabolic processes at the cellular level and are manifested in the whole plant. However, the degree of tolerance and adaptability to abiotic stresses may differ across species and cultivars of crops [2]. It is necessary to understand the adaptive mechanisms of plants to identify traits associated with tolerance to abiotic stresses. Several proteins and genes involved in abiotic stress adaptation and mitigation have been integrated to develop varieties that are tolerant to abiotic stresses [3–6]. The genetic engineering of crop plants with stress-responsive genes has been demonstrated to enhance the adaptation to various abiotic stresses [1,7–9]. Much of the gene identification efforts can be traced to model plants like *Arabidopsis*, and this basic knowledge needs to be accelerated to make the crop plants resilient to abiotic stresses in target growth environments. There is a need to explore those aspects of stress adaptation that have not been effectively utilized or employed to improve key food grain crops.

Microbes that are associated with plants in natural habitats under diverse environments exhibit tremendous capabilities to cope with stresses caused by environmental factors. Since plants must interact with microbes, microbes are believed to modulate plant defense mechanisms to protect against adverse external conditions [10,11]. With better insights into plants' responses to environmental challenges such as drought, heat, and salinity, improved management practices and tools can be applied to increase stable yields. This review aims to update current knowledge about the impacts of key abiotic stresses in major cereal and legume crops, the mechanisms of tolerance to various abiotic stresses, and the opportunities to translate the knowledge for the development of climate-resilient crop varieties and management practices.

2. Abiotic Stresses and Their Impacts on Grain Crops

Plants experience abiotic stresses when they are exposed to supra- or sub-optimal levels of environmental factors such as temperature, soil moisture, and salts in the soil [12,13]. It is increasingly realized that climate change will lead to a decline in crop productivity, mainly by enhancing the frequency and intensity of abiotic stresses such as extreme temperatures, droughts, salinity, and waterlogging. The ability of crops to cope with these challenging situations is the crucial aspect of abiotic stress resilience and stable crop productivity. Hence, genetic improvement has long been a target for crop scientists to make crops more resilient to stresses. There is a need to accelerate the current efforts to develop stress-tolerant genotypes, with a focus on the traits that contribute to the abiotic stress tolerance and grain yield, which is conventionally preferred. This process would be driven by our knowledge about plant mechanisms to survive and grow under the constant changes and extreme environmental conditions at the whole plant, organ, tissue, and cellular levels (Figure S1) [3,14–20].

2.1. Drought

Droughts are a major challenge faced by most food crops that are sensitive to a soil moisture deficit. The impact of droughts on the final yield and various physiological and biochemical processes of crops depends on its intensity, timing, and duration (Tables 1 and 2). However, its impact is lessened in the cases of adopted and evolved crops under the harsh conditions of semi-arid and arid regions [21]. Both the vegetative phase, as evident from leaf growth, and the reproductive phase, as evident from floral development, is severely affected due to soil moisture deficits [22,23]. The timing and duration of water stress determines the impacts on developmental processes, as evident from changes in the duration of flowering if stress is applied at the early stages of growth, and a reduction in the grain filling duration if the stress occurs at early or terminal reproductive growth stages [23,24]. Extreme drought conditions impair crop morphology, physiology, and

duration, while the moisture content plays a vital role in germination as it affects the enzyme activation that determines plant sensitivity during germination. The occurrence of droughts when the grain filling rate is at its peak can accelerate the leaf senescence and result in smaller grains [23,25]. There is a considerable tolerance range to drought stress across the cereals and legume crops and their cultivars [26,27].

Table 1. Effects of drought stress on yield of different cereal and legume crops.

Crop	Stress Description	Yield Losses (%)	Reference
Wheat	~40% water deficit	20–25	[28,29]
	No irrigation at reproductive and grain filling stages	30–32	[30]
	The different deficit moisture level	25	[31]
Rice	Soils dried beyond –20 kPa	23	[32]
	Withholding water at flowering (-30 ± 5 kPa)	23–24	[33]
	Moderate to severe stress at flowering	51–60	[34]
	Drought, water stress (~40% water deficit)	>50	[29]
	The different deficit moisture level	25	[31]
	-40 and -80 kPa during flowering and grain filling, respectively	34–66	[35]
Maize	50% FC at tasselling stage	20	[36]
	Progressive drought at vegetative stages	19–26	[37]
	Progressive drought at reproductive stages	42–47	
	Different irrigation regimes	34–66	[35]
	Drought with approximately 40% water reduction	39.3	[28]
Barley	Water stress (20% and 60% FC) during grain filling	50–60	[38]
	Drought stress at the start of anthesis (Field capacities 30%)	42	[39]
Pearl millet	Early drought stress from 3 weeks after germination for four weeks	>50	[40]
Millets	Rainfed conditions associated with terminal drought	53	[41]
Chickpea	Withholding water at reproductive stage	30–40	[42]
	Withholding water at early podding	80–90	[43]
	Under rainfed conditions with lifesaving irrigation	27	[44]
Beans	Withholding water after 25 days	80	[45]
Pigeon pea	Drought at flower initiation, soil moisture reduced from field capacity of 16% to 5.6%	11–40	[46]
Soybean	Rainfed in comparison to fully irrigated	33	[47]
	4 days of moisture stress during seed filling stage (R4–R6)	39–45	[48]
Black gram	Irrigated to FC when the weight of each pot reached 50% of FC	23	[49]
Mung bean	Withholding the irrigation at blooming stage to maturity stage and seed filling stage	51–85	[49]

Table 2. Physiological and biochemical responses of plants under drought stress.

Crop	Stress Description	Trait/Organ Affected/Impact	Reference
Rice	Soils dried beyond−20 kPa	Yield loss~22.6	[32]
Wheat	Drought, water stress (~40% water deficit)	Yield loss~25	[29]
Maize	5 days of drought stress at the V9 stage and 5 days after pollination stage by maintaining 14.0–15.0% SWC	Reduced kernel size, reduced expression of photosynthesis genes, and reduced yield	[50]
	Short-duration water deficits during the rapid vegetative growth period	28–32% loss of final dry matter weight	[51]
Sorghum	Season-long drought stress	Decreased harvest index, seed numbers, and seed size	[52]
Millets	Irrigation with mannitol (200, 400, and 600 mM) for 21 days at an interval of three days	Decreased germination, RWC; chlorophyll content increased root growth, proline, and MDA content	[53]
Chickpea	Drought, water stress for 3 weeks (40% of FC) at vegetative and flowering	Decrease in relative chlorophyll content, RWC; accumulation of H ₂ O ₂	[54]
Pigeon pea	20 days at flowering and pod setting	Flower drop and decreased flower to pod conversion	[46]
Black gram	40% of field capacity	Reduced plant growth, branches, pod numbers, shoot and root dry weight, rate of photosynthesis and transpiration, stomatal conductance	[55]
Soybean	Withholding irrigation at critical stages	Reduced shoot biomass and seed yield, fewer seed pods, and seeds	[56]
Bean	Withholding irrigation after 25 days in field conditions	Reduced leaf area index, harvest index, pod partitioning index	[45]

2.2. High Temperatures

Projected increases in higher ambient temperatures worldwide are likely to drastically reduce crop productivity [1,23,57]. The rise from the seasonal average temperature by 1 °C was shown to reduce cereals' grain yields by 4.1% to 10.0% [58]. High temperatures can lead to a shorter crop life cycle and, hence, a reduction in cereals' productivity [23,59–61]. In wheat, reductions in grain yield [23,62–64] and quality [65] have been reported. This is mainly due to accelerated development [66], reduced photosynthesis [67], and the direct impacts on reproductive processes [23,59]. Losses in grain yields due to high temperature stress on selected cereal and legume crops are shown in Table 3. The tolerance to high temperatures in rice is relatively higher at the early growth stage; however, the crop is highly vulnerable to elevated temperatures at later stages, particularly at flowering [59,68,69]. The high sensitivity of the reproductive stage has been reported even in recently released cultivars of wheat [70]. Sensitive stages and temperature thresholds of key cereals crops such as wheat [71], sorghum [23,72], and finger millet [73] are well quantified. Similarly, the impact of high temperature stress on various physiological, growth, reproductive fertility, and yield components are well documented for major cereals such as rice [68,74], wheat [71,75,76], sorghum [77,78], and pearl millet [79]. Similarly, the impacts on major legume crops are also well documented for crops such as the chickpea [80,81], black gram [82], green gram [83], kidney bean [84], soybean [85], peanut [86–89], and lentil [90,91]. The key effects of heat stress on selected crops are summarized in Table 3.

Table 3. Effects of high temperature stress on different crop species.

Crop	Temperature	Growth Stage	Effect	Reference
Rice	40 °C	Emergence	Delay and decrease in the emergence	[92]
Wheat	45 °C		Reduced chlorophyll, photosynthesis, protein synthesis	[71,93–96]
	30/25 °C, day/night >32/22 °C, day/night		Green leaf area and productive tillers/plant reduced Decreased photosynthesis, membrane damage, floret fertility, seed numbers, seed size	
Maize	35/27 °C in day/night 14 days before reproductive to silking stage		Decreased cob weight, low sugar content	[97]
Sorghum	40/30 °C, day/night; 38/28 °C		Lipid peroxidation of chloroplast and thylakoid membranes; decreased floret fertility, grain weight	[23,77,78,98–102]
Pearl millet	>36/22 °C day/night	Emergence to maturity Booting to maturity	Decreased days to flowering, seed yield, and seed size; decreased pollen germination, numbers of seeds per panicle, and seed yield per panicle	[79]
Finger millet	>36/22 °C day/night	10 d after emergence through maturity	Decreased plant height, tillers, seeds per fingers, and grain yield	[73]
Chickpea	Gradual 29/16 C to 40/25 °C	Flowering	Lower pollen production, % pollen germination, pod set, and seed numbers	[103]
Black gram	40 °C	Flowering and pod setting	Reduced yield	[82]
Green gram	40 °C 60 days	Reproductive	Reduced yield	[83]
Common bean	32/25 °C	V4 until physiological maturity	Increased photosynthesis, conductance, and leaf area	[104]
	>28/18 °C	Emergence to maturity	Decreased seed-set, seed number per plant, seed number per pod, seed yield, and total dry weight per plant	[84]
Soybean	38/28°C (day/night), 14 days		Lower photosynthesis, stomatal conductance (gs), damaged membranes (chloroplast, thylakoids, mitochondria), and increased leaf senescence	[85,105,106]
Peanut	>32/22 °C	Flowering	Decreased fruit-set, pollen production, pollen viability, and pod numbers per plant	[86–88]
	>32/22 °C	Emergence through maturity	Decreased pollen viability, seed-set, seed number pod, seed size, and harvest index	[89]

High temperatures affect photosynthesis and its components in rice [107], wheat [108], maize [109], beans [110], and the chickpea [111]. On the other hand, an increase in respiration, rather than photosynthesis, was conspicuous in bean genotypes in response to

elevated temperatures [112]. Heat stress differentially affects the stability of various proteins, membranes, RNA species, and cytoskeleton structures, and it alters the efficiency of enzymatic reactions in the cell [58,113]. Every plant's growth stage is susceptible to heat stress, but the reproductive stages are the most vulnerable. A slight increase in temperature during flowering may lead to a loss of grain yield. The failure of grain formation and development can be attributed to impaired pollen germination, pollen tube growth, and reduced ovule viability, as well as anomalies in stigmatic and style positions, a reduced number of pollen grains retained by the stigma, impaired fertilization processes, obstacles in the growth of the endosperm, and unfertilized embryos or embryo abortions as reported in rice [114], wheat [115], the chickpea [80] and other grain crops [59]. High temperatures can change nutrient uptake patterns as seen in pearl millet, which can accumulate more N, P, and K relative to unstressed plants, but the uptake of Ca^{2+} , Mg^{2+} , Na^+ , and S remains unaffected [116].

2.3. Salinity

Salinity is a significant abiotic stress that restricts crop growth and productivity and is characterized by an excessive concentration of soluble salts in the soil that suppresses plant growth in many irrigated, arid, and semi-arid regions of the world [117]. The extent of the salt injury depends on the crop species, cultivar, growth stage, any ecological factors, and the nature of the salts in the soil. The physiological and biochemical responses of plants under salinity stress are shown in Table 4.

An increase in the EC above 0.88 dS m^{-1} led to a decrease in rice grain yield [118]. The grain yield loss of wheat genotypes in response to salt stress was as high as 82% in controlled environmental studies [119]. Salinity can adversely affect seed germination in rice [120], wheat [121], maize [122], the faba beans [123], the chickpea [124], and the mung bean [125,126]. This is due to the high osmotic potential outside the seed, inhibiting the absorption of water, or due to the toxic effects of Na^+ and Cl^- . High Na^+ concentrations prevent the absorption of K^+ ions, which are highly essential for growth and development [127].

The interference of salts with the nutritional homeostasis of plants increases ionic ratios such as Na^+/K^+ , $\text{Na}^+/\text{Mg}^{2+}$, $\text{Na}^+/\text{Ca}^{2+}$, $\text{Cl}^-/\text{H}_2\text{PO}_4$, and $\text{Cl}^-/\text{NO}_3^-$, which adversely affects plant cellular processes [128,129]. Crop species and cultivars widely vary in their tolerance to salinity. For example, durum wheat is more sensitive to salt than bread wheat at critical growth stages such as at germination and early growth [130]. These differential responses of durum and bread wheat are due to differences in their ability to eliminate Na^+ from the leaf and to discriminate between K^+ and Na^+ . It is well-known that salinity affects plant growth through low soil solution osmotic abilities and nutritional imbalances [131]. In cereals, it alters plant growth through ionic imbalances, oxidative alterations, metabolic regulations, nutritional disorders, membrane disorganization, and low cell differentiation rates in crops like rice [132], wheat [133], maize [116], and the chickpea [134].

2.4. Waterlogging

Waterlogging and submergence causes substantial yield losses in food grain crops. Climate change scenarios predict increases in future incidences and intensities of floods, especially in the tropics and subtropics [144]. Most dryland cereals such as maize, wheat, and barley are sensitive to waterlogging, causing up to 20% yield losses in irrigated areas and even more significant losses in rainfed ecosystems exceeding 40% [145]. Damage estimated up to 100% may be caused by waterlogging stress, depending upon the crop, the length of the waterlogging, and the stage of plant growth. Based on the height of the water, the flood can be categorized as waterlogging when it is superficial and covers only the root, or it can be categorized as submergence when the water completely covers the aerial tissues of the plant [146].

Table 4. Physiological and biochemical responses of plants under salinity stress.

Crop	Salinity Level	Effect	Reference
Rice	EC 10 dS/m	Decreased root and shoot length	[135]
Wheat	100 to 175 mM NaCl	Reduction in spikelets per spike, delayed spike emergence and reduced fertility	[136]
Maize	1, 50, 100 mM NaCl	Stunted growth, reduced chlorophyll fluorescence, and enhanced levels of reactive oxygen species and 1,4-benzoxazin-3-one aglycones (aBX)	[137]
Millet	100, 200, and 300 mM NaCl	Depression in germination percentage, shoot and root growth rate, leaf relative water content, chlorophyll content, leaf K ⁺ concentration	[138]
Chickpea	0, 4, 6, and 8 dS m ⁻¹	Reduced dry matter accumulation in root and shoot	[139]
Pigeon pea	0.5 to 4.3 dS m ⁻¹	Height, biomass, SSL, and RGR linearly decreased	[140]
Black gram	150 and 225 mM of NaCl	Reduction of leaf, shoot, and root biomass	[141]
Green gram	50 mM and 75 mM NaCl	Reduction in plant height, total chlorophyll, carotenoid contents, plant length, leaf area, rate of photosynthesis, yield characteristics	[142]
Common bean	100 mM NaCl	More lipid peroxidation, electrolyte leakage, abscisic acid (ABA); lower seed germination percentage, seedling growth, cell membrane stability index, and relative water content	[143]

Underwater plant cells that carry out photosynthesis do not readily exchange oxygen and CO₂. Therefore, flood-damaged plants have a lower rate of aerobic cellular respiration than normal plants. Low CO₂ concentrations in flooded leaves subsequently limit photosynthesis. Flooding leads to an energy crisis within the cells of plants [147]. Waterlogging leads to hypoxic or anoxic conditions in the soil, in which the soil becomes devoid of oxygen. The lack of oxygen for root respiration reduces the rate of root growth. Soil toxicity prevents root development and encourages root decay.

The waterlogging reduces photosynthesis due to stomatal closure, as well as abscisic acid (ABA), ethylene, and active oxygen species production. In addition, stomata closure often restricts CO₂ in plant cells and induces the accumulation of oxygen free radicals. Plants under waterlogged conditions experience increased cellular damage from reactive oxygen species [148].

3. Combined/Multiple Stresses

Plants are constantly exposed to various environmental stresses such as salinity, drought, cold, and high temperatures. The impact of abiotic stresses on the grain yield of cereals and legumes is shown in Table 5. These multiple and combined stresses can vary in duration and intensity and can act simultaneously or sequentially. Earlier stress interactions have a significantly higher negative impact on crop productivity than each of the different stress components applied individually [149]. Drought and heat stress are excellent examples of two distinct abiotic stress conditions in the field simultaneously. This combination has a significantly greater detrimental effect on the growth and productivity in crop plants as compared to stresses applied individually [150]. Negative interactions have also been demonstrated in plants subjected to high intensity light and drought [151], high intensity light and cold stress [152], and drought and high temperatures [153,154].

In comparison, relative to each of the stresses applied separately, certain stress combinations may benefit plants. Examples include elevated CO₂ levels, which are advantageous when combined with other stresses such as salt or high light [155]. Salinity in combination with heat stress in tomatoes enhances the protection against the damaging effects of salinity, suggesting that the accumulation of osmoprotectants such as glycine betaine and trehalose could play an important role in protecting plants against stress combinations. Combi-

nations of drought and ozone could decrease the ozone intake in stomata by reducing stomatal conductance because of drought stress [156].

Table 5. Impact of abiotic stresses on grain yield of cereals and legumes.

Stress	Growth Stage	Crop	Details of Abiotic Stress	Decrease in Yield (%)	Reference
High temperature	After heading	Wheat	>31 °C	16–25	[157]
			Delayed sowing in the field Minimum temp. 15–21 °C Maximum temp. –31–36 °C	22	[158]
	Heading	Rice	Diurnal temp 24–32 °C (control) 26–39 °C (high temp.)	21–55	[159]
	Tasseling stage	Maize	28/20 °C (control) 38/30 °C (high temp.) for 15 days	7–17	[36]
	Emergence to maturity	Sorghum	32/22 °C to 36/26 °C 32/22 °C to 40/30 °C	10 99	[160]
	Booting to start of seed filling	Pearl millet	28/18 °C to 36/26 °C 28/18 °C to 40/30 °C	50 98	[79]
	Emergence to Maturity	Finger Millet	32/22 °C to 36/22 °C 32/22 °C to 38/28 °C	75 84	[73]
	Emergency to Maturity	Chickpea	<32 °C/20 °C (control, normal sown) >32 °C/20 °C (high temp, late sown)	19–56	[81]
	Reproductive stage	Lentil	38/23 °C	85–88	[161]
	Reproductive stage	Mung bean	>40/25 °C	35–40	[83]
Emergence to Maturity	Kidney Bean	>28/18 °C to 40/30 °C	6.5% per 1 °C	[84]	
Flowering	Peanut	36–44/26–34 °C	14–90	[89]	
Salinity	Vegetative	Mung bean	50 mM and 75 mM NaCl	41–75	[142]
	Throughout crop duration	Wheat	0–200 mM NaCl	25–70	[162]
	Throughout crop duration	Faba bean	0.7, 3.0, and 5.0 dS m ⁻¹	27–47	[163]
	Throughout crop duration	Chickpea	0.7, 3.0, and 5.0 dS m	40–56	[163]
		Rice	3.8 to 6.4 dS m ⁻¹	~50	[164]
	Seedling and reproductive	Rice	4 dS/m ²	28.8	[165]
Waterlogging	Vegetative or reproductive	Wheat	Early or late waterlogging for 14 days	14–29	[166]
	Vegetative or reproductive	Barley	Early or late waterlogging for 14 days	15–21	[166]
	Vegetative	Oats	0–35 days	79–83	[167]
	Vegetative/heading	Wheat	Flooding	30.4–39.4	[168]
	Vegetative or reproductive	Field pea	Early or late waterlogging for 14 days	94	[166]
	Seedling (V3), jointing (V6), and tasseling (VT) stages	Maize	Waterlogging (3, 6, and 9 days) and subsurface waterlogging (5, 10, and 15 days)	61.5–80.5	[169]

4. Mechanisms Associated with Stress Tolerance

Plants are constantly under pressure from environmental stresses, and they tolerate or resist stress by various adaptation and acclimation mechanisms. Plants have evolved complex physio-biochemical and molecular strategies to neutralize the effects of abiotic stress [170,171]. The responses of plants to stress include changes in physiological processes such as photosynthesis, changes in ion levels, changes in membrane fluidity, the accumulation of osmolytes, the synthesis of secondary plant metabolites, phyto-chelation, the activation of ROS scavenging machines, and more. Broadly, there are two groups of stress-responsive genes which protect crop plants from abiotic stresses. One group includes regulatory genes, and the other group includes biosynthetic and structural genes.

4.1. Adaptations to Drought Stress

Plants adapt to droughts by adjusting their phenology, morphology, and physiology at the cellular and molecular levels. The drought-induced inhibition of growth as well as yield reductions can be attributed to adverse effects on plant functions and processes, particularly plant water uptake, water use efficiency, and the partitioning of biomass to grains.

4.1.1. Escape Mechanisms

Plants, including cereals and legumes, tend to escape droughts by curtailing the crop growth duration or accelerating phenological phases, referred to as a flexibility in phenology [172]. This feature has been utilized to develop short-duration drought-tolerant crop cultivars (e.g., rice, wheat, sorghum, the pigeon pea, the peanut, the chickpea, and the lentil). However, severe and prolonged droughts can reduce the grain yields of these crops drastically. In plants that utilize escape mechanisms, seed or pollen germination usually occurs before acute water shortage. However, plants with growth plasticity seem to grow slower in the dry season with few flowers but have more fruits and seeds in the normal season.

4.1.2. Dehydration Avoidance

The plant adjusts to droughts by lowering water loss and getting more water through root uptake. Adaptive traits are used to set the background of a “low transpiration rate in water-saving plants” and an “osmotic adjustment in water-spender plants” to prevent dehydration [173,174].

Plants mostly rely on leaf relative water content, osmotic adjustments, and root architecture to enhance the yield under drought stress [175]. Reducing the size of the leaves can be regarded as a mechanism to minimize water loss by transpiration. It has been documented that leaf shedding occurs from the oldest leaves to the youngest leaves during sequential water shortages, and drought-tolerant genotypes have higher leaf-shedding rates [176]. Closed stomata also suggest drought tolerance because in response to drought stress, stomata are closed, and transpiration is decreased [177]. Water loss is significantly influenced by the stomatal movement, stomatal density, and the resistance of plants to transpiration. Remarkable variations in the stomatal functions of various plants during droughts have been identified [178,179]. Adaptations to droughts can reduce the stomata size or the number of stomata. These unique anatomical features were created to protect the plant from harsh environmental conditions. Plants from arid and semi-arid habitats show sunken stomata, protected by resinous layers, waxes, and detritus on the laminae that sticks to stomata [180].

Drought-tolerant plants exhibit adaptive root properties, including long roots, high densities of roots, and intense rooting systems [177,181,182]. Plants selectively produce and extend their roots towards the wet part of the rhizosphere due to specific genes associated with this process [183,184]. Denser roots can absorb greater amounts of water because of the more extensive root system [185]. The gene responsible for root hair elongation is associated with drought tolerance in maize [186], rice [187], wheat [188], and grain legumes [5]. Drought tolerance is the plants' ability to tolerate low tissue water content

by adaptive traits, including preserving cell turgor by osmotic adjustment, preserving cell elasticity, and improving protoplasmic resistance. The antioxidative system that operates in response to abiotic stress can also contribute to dehydration tolerance.

4.1.3. Osmoregulation

The cellular dehydration of tissues occurs when plants are exposed to extreme temperatures, droughts, and salinity. The plant cell produces osmolytes such as sugars, proteins, nucleic acids, and amino acids to protect from dehydration, as reported in wheat [189]. An osmotic adjustment is the process of solute accumulation mechanisms in plant cells when the water potential is limited, which helps maintain the turgor. The accumulation of osmotic substances is controlled by the intricate cellular processes involved in water flux and osmotic adjustment during abiotic stress conditions [190]. Sugars are critical biomolecules involved in various crucial physio-chemical mechanisms, from seed germination to senescence in cereals and grain legumes [191]. Sugars play diverse roles such as osmolyte biosynthesis, as well as maintaining membrane integrity, growth, and differentiation [192]. Proline is a compatible osmolyte that protects the cellular machinery from oxidative damage and maintains the homeostasis of photosynthesis [193]. Amino acid-derived compounds such as glycine betaine and polyamines also contribute to abiotic stress tolerance in various plants, including rice [194,195]. The accumulation of these osmolytes in the cytosol is an essential stress response to adjust the osmotic equilibrium in the plants under abiotic stress [194].

4.1.4. Antioxidant System

Reactive oxygen species (ROS) such as singlet oxygen, hydrogen peroxide, superoxide, and hydroxyl radicals are involved in various cellular functions [196,197]. ROS, which exist at a low level under normal conditions, tend to increase when plants are exposed to stress. At high levels, ROS are toxic to cells, while the same molecule at low concentrations can function as a signal transducer that activates a local and systemic plant defense response against stress [198]. Chloroplasts, peroxisomes, endoplasmic reticulum (ER), mitochondria, and apoplasts after exposure to any stress may rapidly produce ROS, which are dangerous to the plant if not mitigated or scavenged. Plant peroxisomes are considered as a factory of ROS and a regulator of NO and H₂O₂ metabolism [199]. Rezayian et al. [200] reported that NO stimulates the antioxidant system and osmotic adjustment in the soybean under drought stress. Biswas [201] reported that ROS and reactive carbonyl species constituted a feed-forward loop in auxin signaling and play an important role in lateral root formation. Vanillic acid [202,203], selenium [102,204] and cerium [101] also play roles in antioxidative defense mechanisms in plants.

The plant possesses antioxidant machinery with the enzymatic and non-enzymatic components to mediate redox signaling and ROS homeostasis linked to acclimation responses to abiotic stressors. In response to stress, several antioxidative enzymes are produced by the plant. Superoxide dismutase (SOD), catalase (CAT), and peroxidases (POX) are among the enzymatic components of antioxidant systems that regulate the homeostasis of ROS within organisms, as reported in wheat [95,205], rice [206], sorghum [77,100,101], pearl millet [79] and the chickpea [6]. The non-enzymatic antioxidants include components such as ascorbic acids, α -tocopherol, flavonoid, glutathione, and carotenoids, which efficiently alleviate oxidative damage by reducing ROS activity or by working together with the enzymatic players to achieve efficient antioxidant activity via the utilization of H₂O₂ [207–209]. The ascorbate–glutathione pathway comprises of AsA, GSH, and four enzymes, viz. ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase, which play vital roles in detoxifying ROS and ultimately mitigate oxidative damage in plants under abiotic stress [210].

At the cellular level, singlet oxygen, superoxide, hydroxyl ion, and hydrogen peroxide (H₂O₂) generation are typical heat stress incidents [211]. To defend against the damaging effects of the over-production of ROS under heat stress, plants have evolved complex

antioxidant enzymes and non-enzymatic antioxidants, as reported in many crops such as wheat [61], the chickpea [212], and the pigeon pea [213]. The involvement of nitric oxide in ROS generation has been associated with abiotic stress tolerance [214].

4.1.5. Phytohormones

Plant hormones play pivotal roles in controlling responses to several internal and external stimuli. Abscisic acid (ABA) is the key hormone considered to regulate the response of plants to abiotic stresses. Increased levels of endogenous ABA under drought stress conditions have been reported in many plant species, which include grain crops like sorghum [215], rice [216], barley [217], the soybean [218], and wheat [219]. The level of ABA is also influenced by cold stress in wheat [220], heat stress in wheat [115,221,222], and salt stress in maize [223]. ABA accumulates in stressed plants, interrupts their photosynthesis, and stimulates stomata closure to reduce water loss through transpiration. The roles of ABA in abiotic stress tolerance have been reported in a variety of plant species through its exogenous application either as foliar spray or as a seed primer in different crops, including cereals and legumes [224–226].

The exogenous application of ABA may also increase responses to droughts in wheat [227,228]. ABA is considered to have a beneficial impact on stress resistance after exogenous applications or by overexpressing genes due to its increased endogenous content in plants. ABA induces the expression of several genes whose products are essential for stress and tolerance reactions, such as osmo-protective synthesis enzymes [229]. Under drought conditions, ABA is synthesized in the roots and exported to shoots, as well as causing stomatal closure. The exogenous applications of auxin [230] and ethylene [231] are also effective in increasing abiotic stress tolerance; however, doses and stages are species-specific. Seed priming with auxin [232] and GA [233] was found to reduce the adverse effects of drought stress on yields, and was associated with improved physiological functions.

Cytokinin (CK) postpones the premature senescence of leaves and death during drought stress and promotes adaptive traits that help enhance grain yields. The increase in endogenous levels of CK through the expression of the CK biosynthesis gene isopentenyl transferase (*IPT*) delays cell senescence caused by droughts and improves crop yields [234]. In addition to controlling root growth and branching, CK inhibits the primary root growth and branching under drought stress [235]. Jasmonic acid also plays a vital role in abiotic stress tolerance, mainly in drought stress in plants [236].

4.2. Adaptations to High Temperature Stress

Plants adapt to high temperature stress through morphological and physiological adjustments. Mechanisms may vary across the crop growth stages. Critical growth stages such as anthesis and grain filling are highly sensitive to above optimum temperatures. Some adaptation mechanisms to cope with high temperature stress includes canopy cooling through transpiration, the involvement of heat shock proteins, various endogenous protectants, the antioxidant system, and the regulation of the biological clock, as reported recently.

4.2.1. Transpirational Cooling

To cope with elevated ambient temperatures, plants transpire more water to maintain the requisite optimum and cooler canopies for physiological function. The mechanisms of transpirational cooling in response to high temperatures and its implications have been comprehensively illustrated [212,237–246]. This is an avoidance mechanism that allows the plant to function and maintain cooler canopies. However, this requires the availability or access to soil water resources and irrigation.

4.2.2. Heat Shock Proteins

High temperature stress leads to the production of a group of proteins called heat shock proteins (HSPs), or stress-induced proteins. Plants under stress tend to produce less

normal proteins and up-regulate genes associated with HSPs [206]. About 20 HSPs have been found in plants, and the diversification of these proteins reflects the adaptation or tolerance to heat stress. The general function of HSPs is to serve as molecular chaperones that control the folding and aggregation of proteins and the localization and degradation of all plants. As chaperones, these proteins avoid the irreversible aggregation of other proteins and engage in protein refolding under heat stress conditions [247]. The HSPs protect cells from damage and make them easier to recover after returning to normal growth conditions. Under high temperature stress, some high molecular weight HSPs, such as HSP101, were recognized as the important proteins for high temperature responses in crop plants like maize [248]. Low molecular weight HSPs, i.e., –18.1 and –17.9, were reported to accumulate in the pea while it was treated for four hours at 42 °C. The changing responses and expressions of the HSPs vary in different phases of development [206]. HSP90 also showed an increased expression under heat stress in rice and the soybean [249]. The involvement of HSPs have been reported in legume crops like the mung bean [250], common bean [251], and in the pigeon pea [252]. The crops where HSPs were involved in a high temperature response that was reported recently included rice [253], wheat [254], and the chickpea [255].

4.2.3. The Role of Protectants

Exogenous applications of osmoprotectants, phytohormones, signalling molecules, and trace elements have shown positive impacts on plants grown under heat stress, as they have growth-promoting and antioxidant abilities. The heat tolerance in plants may be increased by the exogenous application of osmoprotectants [256]. Several different endogenous compounds have been found to be effective in moderating the intensity of heat stress in plants. Tocopherol, a key lipid-soluble redox buffer, acts as a scavenger of singlet oxygen species and other ROS and helps in mitigating heat stress in plants [257], as reported in rice seedlings [258] and wheat [259]. Ascorbate also has the potential to improve heat stress tolerance in maize [111,260]. The primary function of ascorbic acid is to prevent ROS activity and the photoinactivation of PSII and thus prevent the entire photosynthetic apparatus from damage [261]. Compounds like jasmonic acid can alleviate high temperature-induced spikelet-opening impairment during anthesis by enhancing antioxidant abilities and osmotic regulation as reported in wheat [262] and maize [263].

4.2.4. The Role of ROS and Antioxidants

At the cellular level, singlet oxygen, superoxide, OH, and hydrogen peroxide (H₂O₂) generation and reactions are typical heat stress incidents [211]. The production of ROS damages the membranes of several organelles and structures of cells, making them dysfunctional. To defend against the damaging effects of the over-production of ROS under heat stress, plants have evolved complex antioxidant enzymes and non-enzymatic antioxidants as reported in wheat [61], sorghum [77,101,102], the soybean [85,105], the chickpea [212], the pigeon pea [213], and the moth bean [264]. The involvement of nitric oxide in ROS generation has been associated with abiotic stress tolerance [214]. Generally, there is a balance of ROS production and antioxidants under normal conditions. However, under stress conditions, the production of ROS is greater than the antioxidants, leading to the accumulation of ROS, which damages various membranes and limits the functionality of the cell.

4.2.5. The Biological Clock

The temporal effects of thermal stress during the plant's life cycle and the diurnal cycle are critical, and plants have mechanisms to sense peak periods of stress and exhibit appropriate adaptive strategies. Recently, it has been reported that high temperature stress can influence plants' biological clocks, which affects genes associated with the plant's time sensing mechanisms [265]. Wu et al. [266] reported the association of PePIF3a, a positive regulator in plants' drought and salt stress responses, with circadian rhythms. The time of

day of flowering or early morning flowering is a mechanism adopted by some crop species or genotypes to escape heat stress. These crops and genotypes flower early and complete the process of pollination and fertilization early in the morning or during the cooler times of the day before the daytime higher temperatures are reached [59,68,96,114].

4.3. Adaptations to Salinity Stress

Unlike high temperatures and droughts, stresses caused by salinity are not periodic. Plants must cope with the high level of salts in soil throughout their life cycle, though events of precipitation may change the adverse impact of salts depending on soil characteristics. Hence, plants have adaptive mechanisms for both osmotic stresses and the toxic effects of excess ions.

4.3.1. Ion Transport and Homeostasis

Salinity contributes to two types of stress in plants. Osmotic stress occurs at the initial stage due to less water in the soil and the increased cytosolic Na⁺ and chloride in the matured leaves at later stages [267,268]. The maintenance of ion homeostasis by ion uptake and compartmentalization is essential for growth during salt stress, and ion transporters play a crucial role in this process in many crops [269], including rice [270], maize [271], wheat [272] and the chickpea [273]. Excess salt in the plant is partitioned into the cell vacuole or deposited in old tissues and is soon excreted from the plant to protect it from salt-related stress. The superiority of bread wheat over durum wheat has been attributed to the differential ability to sequester sodium in vacuoles in roots [274,275]. Under stressed conditions, the survivability of the plant depends upon the activity of V-ATPase [276], as shown in wheat [277] and barley [278].

The salt-sensitive species in crop plants, such as rice [279], cannot regulate Na⁺ transport at high salinity levels, where ionic effects dominate the osmotic effects. Plant cells need to maintain high K and low Na⁺ levels [280]. Thus, salinity stress tolerance requires maintaining osmotic homeostasis and ionic homeostasis. In general, to survive under high salinity conditions, the plant either adopts avoidance or tolerance mechanisms for osmotic homeostasis and ionic homeostasis. The main adaptive tolerance mechanisms for salinity stress involve successfully eliminating excess Na⁺ ions from the cytoplasm, and its accumulation within the vacuoles [131]. A central mechanism controlling the tolerance of plants to salt stress is the ion compartmentalization of different tissues and cells. Sequestering more Na⁺ in the root and flag leaf sheath in tolerant wheat genotypes can maintain lower Na⁺ concentrations with higher K⁺/Na⁺ ratios in photosynthetically active flag leaves [281]. Excess salt triggers the cytosolic Ca²⁺ concentration, which activates the Ca²⁺ binding proteins and upregulates the Na⁺/H⁺ antiporter to remove Na⁺ [282]. Intracellular Na⁺/H⁺ antiporters mediate the compartmentalisation of Na⁺ in cell vacuoles. The NHX is an antiporter that regulates the cell pH and preserves the homeostasis of Na⁺/K⁺ in plants. It also plays an important role in cell volume control which is needed for sequestering.

4.3.2. Compatible Solutes

Under salinity stress, plants can synthesize compatible solutes to ensure their survival. These compounds include glycine betaines, amino acids, polyols, non-reducing sugars, and polyamines [283]. Some amino acids such as cysteine, arginine, and methionine decrease in a salty environment while proline levels increase. The accumulation of proline is a well-known process to relieve salinity stress. Intracellular proline not only provides resilience to stress but also plays a crucial role in stress recovery. The modulation of the proline metabolism for tolerance to salt and droughts has been reported [284]. It has been documented that reduced forms of sugar, such as glucose and fructose, serve as osmoprotectants under salinity stress. Glycine betaine allows for variations in promoting the alteration of osmoticum by discriminating against Na⁺/K⁺, thereby preserving induction and retaining membrane stability, which significantly reduces sensitivity to salinity [285]. Munns et al. [286] have comprehensively reviewed osmotic adjustment mechanisms and

energy requirements for driving this process. Small molecules such as melatonin have been reported to play a critical role in salt stress tolerance in plants [287,288].

4.4. Adaptations to Excess Submergence and Waterlogging

Plant partial/complete submergence and waterlogging restricts oxygen diffusion to submerged tissues and inhibits aerobic respiration [289]. The decreased oxygen triggers the cessation of the tricarboxylic acid cycle and oxidative phosphorylation. Consequently, the primary source of ATP production shifts from the mitochondrial electron transport chain (ETC) to ethanol fermentation. However, the efficiency of ATP production from ethanol fermentation is lower than that of the ETC. Upon reaeration after a period of oxygen deprivation, ethanol trapped in tissues will be converted to acetaldehyde, causing post-anoxic cell injuries. Furthermore, the concentrations of potentially toxic compounds increase in anoxic soils, and these can enter through roots, damaging both root and shoot tissues. The ROS also accumulate excessively upon oxygen deprivation or re-oxygenation under light conditions [290,291]. Antioxidant enzymes, including superoxide dismutase, catalase, and various peroxidases can effectively reduce ROS activity. Other non-enzymatic components of antioxidants such as ascorbate, glutathione, and β -carotene also play an important role in removing toxic oxygen compounds [290]. Despite these complex sets of detrimental effects posing challenges to the plant in flooded soils, some progress is being made in developing flood-tolerant varieties of cereals, particularly in rice.

Plants have many defensive mechanisms to defend themselves against waterlogging stress, such as forming aerenchyma (aerospaces) in the root cortex, expanding the stem (hypertrophy), forming adventitious roots near the soil surface, and root tip death [292]. Rice has developed specialized anatomical and morphological traits such as aerenchyma, radial oxygen loss barriers, adventitious roots, and the ability to form a leaf gas film to adapt to excess water conditions. However, these strategies are insufficient for survival under continuous and complete submergence, which leads to death due to oxygen starvation. Some Asian rice varieties have further developed additional traits such as aerobic germination, the quiescence of leaf elongation in response to flash floods, and internode elongation under periodic flooding to overcome prolonged submergence [293]. Plants can get their leaves out of the water by growing the shoot above water. This 'escape technique' can be accomplished by high growth in stems, as observed in rice [294]. The possibilities of the modulation of the fermentative and sucrose metabolizing pathways under waterlogging conditions and the genetic variations in these mechanisms have been reported [295].

5. Explored Mechanisms of Abiotic Stress Tolerance for Crop Improvement

In plants, abiotic stress tolerance is a complex trait involving many different metabolic pathways and cellular and molecular components. Abiotic stresses commonly induce various responses at the morphological, physiological, biochemical, and genomic levels. For several decades, the plant research community has amassed a highly comprehensive understanding of the physiological and biochemical mechanisms that facilitate productivity maintenance in response to several abiotic stresses like droughts, flooding, heat stress, cold, salinity, and heavy metals. Understanding the abiotic stress tolerance mechanisms laid the foundation for the development of climate-resilient crop varieties [296]. The conventional breeding approaches have randomly exploited these plant tolerance mechanisms with limited success. Conventional breeding approaches are limited by the complexity of stress tolerance traits and the lowered genetic variation exhibited by most crops due to domestication bottlenecks. Furthermore, abiotic tolerance mechanisms in crop plants are limited and have largely failed to bridge the gap between theoretical research and crop breeding. Therefore, unraveling the genetic, epigenetic, transcriptomic, and metabolomic bases of stress tolerance mechanisms/traits is crucial for breeding climate-resilient or abiotic stress-tolerant crop varieties [297]. However, some success has been achieved in understanding the crop tolerance mechanisms to abiotic stresses, and a few of them have

been explored for crop improvement. Some of the explored mechanisms involved in different methods of abiotic stress tolerance were compiled and presented in Table 6.

Table 6. Explored mechanisms involved in tolerance to different abiotic stresses.

Mechanism/Traits	Genes/Proteins/Enzymes and Other Molecules Involved	Target Crop	Abiotic Stress	Reference
Early flowering	Vernalization (<i>Vrn</i>), photoperiod (<i>Ppd</i>), and earliness per se (<i>Eps</i>) genes; <i>VRN1</i> and <i>Ppd-D1</i>	Wheat	Drought	[298]
	Mutant BW507 line (mutant allele <i>Mat-c</i>)	Barley	Drought	[299]
Osmoprotection and osmotic adjustment	Sugars (glucose, fructose, fructans, and trehalose)	Rice	Salinity	[300]
	Raffinose family oligosaccharides (RFO)	Rice	Cold and Drought	[301]
	γ -aminobutyric acid (GABA)	Wheat	Salinity	[302]
Lignin production (cell wall integrity)	<i>GmRD22</i> (regulates cell wall peroxidases and hence strengthens cell wall integrity under stress conditions)	Soybean and rice	Salt and osmotic stresses	[303]
Scavenging of ROS: Antioxidant Regulation	Enzymatic antioxidants: Catalase and pyrroline-carboxylate synthetase (<i>P5CS</i>), and sustained activities of superoxide dismutase (<i>SOD</i>) and ascorbate peroxidase (<i>APX</i>)	Chickpea	Salinity	[292]
	Non-enzymatic antioxidant compounds: Helicase proteins (e.g., DESD-box helicase and OsSUV3 dual helicase), Ascorbate, Glutathione	Rice Pea	Salinity	[304–306]
Flash flood tolerance	<i>SUB1A-1</i> encoding <i>AP2/ERF</i> (ethylene response factors), family transcription factor	Rice	Flood	[307,308]
Anaerobic germination	<i>OsTPP7</i> encoding Trehalose-6-phosphate Phosphatase	Rice	Flood	[309]
Internode elongation under submergence	<i>SK1</i> (<i>SNORKEL1</i>), <i>SK2</i> encoding, <i>AP2/ERF</i> family transcription factor	Rice	Flood	[294]
Internode elongation under submergence	<i>SD1</i> (<i>OsGA20ox2</i>) encoding, Gibberellin 20-oxidase	Rice	Flood	[310]
Leaf hydrophobicity and gas films are conferred by a wax synthesis gene (<i>LGF1</i>); formation of gas films necessary for gas exchange and underwater photosynthesis	Leaf Gas Film 1 (<i>LGF1</i>)	Rice	Flood	[311]
Traits: Dormancy/quiescence during submergence; reduced elongation growth and carbohydrate consumption during submergence	<i>SUB1</i>	Rice	Flood	[308]
Underwater photosynthesis: Leaf gas films to facilitate gas exchange; supply of carbohydrates to roots for survival, regeneration, and growth	<i>LGF1/OsHSD1</i>	Rice	Flood	[311,312]
Chlorophyll retention under submergence: Blocking ethylene responsiveness; scavenging reactive oxygen species (ROS) to protect chlorophyll and other cellular membranes	<i>SUB1</i>	Rice	Flood	[313]
Chlorophyll retention under submergence: Scavenging reactive oxygen species (ROS) to protect chlorophyll and other cellular membranes	Several scavengers induced during submergence	Rice	Flood	[313,314]

Table 6. Cont.

Mechanism/Traits	Genes/Proteins/Enzymes and Other Molecules Involved	Target Crop	Abiotic Stress	Reference
A barrier to radial oxygen loss (ROL): Minimize oxygen losses in the basal portion of the roots and maximize its delivery to the root apex; minimize uptake of toxins generated in anoxic soils		Rice	Flood	[315,316]
Ion Homeostasis: The excess salt is either transported to the vacuole or sequestered in older tissues which eventually are sacrificed, thereby protecting the plant from salinity stress	SOS1, SOS2, and SOS3 proteins involved in Salt Overly Sensitive (SOS) signaling pathway; SOS1-regulating Na ⁺ efflux at the cellular level. It also facilitates long-distance transport of Na ⁺ from root to shoot. SOS2 encodes a serine/threonine kinase, and is activated by salt stress elicited Ca ⁺ signals. SOS3 is a myristoylated Ca ⁺ binding protein	Wheat	Salinity	[317]
	HKT (histidine kinase transporter) located on the plasma membrane and intracellular/tonoplast-localized NHX-encoding K ⁺ transporters	Rice	Salinity	[318,319]
Polyamines (PA)*: Protect cells from stress-induced damages, membrane integrity, regulation of gene expression for the synthesis of osmotically active solutes, reduction in ROS production, and controlling the accumulation of Na ⁺ and Cl ⁻ ions in different organs. * PA is a small, low molecular weight, ubiquitous, polycationic aliphatic molecule that is widely distributed throughout the plant kingdom.	Diamine putrescine (PUT), triamine spermidine (SPD), and tetra-amine spermine (SPM)	Wheat, barley rice	Salinity	[320,321]
Nitric Oxide: Triggers expression of many redox-regulated genes, preventing lipid oxidation, scavenging superoxide radicals, and formation of peroxynitrite that can be neutralized by other cellular processes; activation of antioxidant enzymes	Sodium nitroprusside (SNP), a NO donor	Maize	Salinity	[322]
Hormone Regulation	ABA: The accumulation of ABA can mitigate the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates; ABA is involved in the expression of several salt and water deficit-responsive genes including <i>HVP1</i> and <i>HVP10</i> genes, <i>TIP 1</i> and <i>GLP 1</i> genes, <i>NCP1</i> and <i>ZmPIF3</i> proteins	Rice Wheat Barley Maize	Salinity and drought	[205,323–326]
	Compounds that have hormonal properties such as salicylic acid (SA), jasmonates, and brassinosteroids (BR)	Rice Wheat Legumes	Salinity and drought	[327–329]

5.1. Early Flowering

Early flowering or maturity (EF/EM) is the most critical phenological trait/mechanism exploited by breeders for the development of short-duration varieties which can escape abiotic stresses, particularly droughts and heat stress. Early flowering and seed set before an upcoming drought event are important in legumes [330] and cereals [298]. This trait is controlled by three groups of genes, vernalization (*Vrn*), photoperiod (*Ppd*), and earliness per se (*Eps*), and the genetics of these traits have been studied extensively, particularly in cereals [331–334]. Shavrukov et al. [298] gave an insight into the early flowering mechanisms and discussed drought escape, with wheat as a target crop. Several studies reported that the crops with EF/EM traits could produce higher and more stable yields under drought conditions [331,335,336]. Furthermore, this is also supported by reports of more seeds under water limitations of EF/EM in pearl millet and sorghum [336,337]. Four cultivars of

the chickpea and seven mutant mung bean lines flowered 2–4 weeks earlier than traditional cultivars and parental forms, respectively, displaying an enhanced seed yield [336].

Matyszczak et al. [299] identified two near-isogenic lines, *BW507* and *BW508*, in barley which were reported to carry two independent early-flowering mutant loci, *mat-b.7*, and *mat-c.19*, respectively. They mapped the mutation in *BW507* to a 31 Mbp interval on chromosome 2HL and concluded that *BW507* has a deletion of *Mat-c*, which is an ortholog of *Antirrhinum majus* CENTRORADIALIS (*AmCEN*) and *Arabidopsis thaliana* TERMINAL FLOWER1 (*AtTFL1*) and is a key gene in regulating early flowering. There is evidence that evolution can favor EF/EM traits in native populations of plants even without the pressure of oncoming drought stress [298]. Zonneveld et al. [338] concluded that during evolution, *Vigna taxa* more easily acquired phenological traits for a short life cycle to escape droughts and heat stresses compared with acquiring physiological traits.

5.2. Root System Architecture

Variations in root system architecture can be explored for the development of climate-resilient and abiotic stress-tolerant crops by improving water and nutrient use efficiency [339]. The primary root elongation rate and ABA accumulation under different water conditions have been studied in 12 maize inbred lines to assess the relationship between root growth and hormonal conditions [340]. Histograms of primary root elongation responses to the varying water deficits suggest multiple mechanisms may be responsible for the response to water stress observed in different maize lines [340]. A recent study on wheat revealed wide variability in root system architecture and shoot traits at the seedling stage in an association panel [341]. The root diameter and the distribution of the metaxylem vessels contribute to drought tolerance in legumes [342].

Phule et al. [343] observed that the formation of fewer aerenchyma, thickened roots, and larger xylem areas were critical anatomical traits associated with aerobic adaptation compared to anaerobic conditions. The photosynthetic rate was significantly higher in the rice cultivar CR Dhan 202 than BPT 5204 under aerobic conditions. The morpho-physiological results showed that the root length, total dry weight, and the photosynthetic rate are the key parameters for aerobic adaptation. These root anatomical and morpho-physiological traits associated with the adaptation can be used as screening criteria for the phenotyping and selection of genotypes suitable for the aerobic cultivation system. This information on morpho-physiological traits is expected to expedite the development of aerobic rice varieties in aerobic breeding programs.

Polania et al. [344] identified seven standard bean lines (SEA 15, NCB 280, SCR 16, SMC 141, BFS 29, BFS 67, and SER 119) that showed greater root vigor under drought stress in the greenhouse, and higher values of grain yields during drought stress under field conditions. Such water use-efficient plant ideotypes (water-spender ideotypes represented deeper root systems, while the-water saver ideotypes showed a relatively shallower root system) could serve as parents for improving drought tolerance in the common bean.

5.3. The Role of Chloroplasts in Plant Abiotic Stress Responses

Photosynthesis in higher plants is sensitive to various abiotic stresses. The photosystem II (PSII) is the most sensitive to desiccation. Its sensitivity could be strongly associated with the desiccation severity [345]. Chloroplasts are semiautonomous intracellular organelles central to photosynthesis and are essential for plant growth and yields. The significance of the function of chloroplast-related genes in response to climate change has not been well studied in crops. The metabolites synthesized in chloroplasts protect plants from abiotic and biotic stresses, including heat, cold, drought, salt, light, and pathogens [346,347]. Through meta-expression analyses under abiotic stress conditions, Yoo et al. [348] identified 264 cold or heat stress-responsive plastid-related genes in rice. Furthermore, the functional characterization of plastid-related genes emphasized the significance of genes for crosstalk between chloroplast development and heat stress. They concluded that chloroplast-related genes affected the abiotic stress response mainly through the high temperature response,

with little effect on responses to droughts and salinity stress. Furthermore, they predicted a protein to protein interaction network analysis associated with high temperature stress which is expected to provide the basis for studying molecular mechanisms by which chloroplasts will respond to different abiotic stresses under changing climatic scenarios. Khurana et al. [349] characterized the chloroplast localized wheat membrane protein (TaRCI) and its role in heat, drought, and salinity stress tolerance. This membrane protein (TaRCI) could be a potential candidate for gene manipulation for improving stress tolerance in crop plants in general, and wheat crops in particular.

5.4. Deficit and Excess Water Stress Tolerance

In recent years, the use of root system architecture for the improvement of stress tolerance in crop cultivars has gained attention. The discovery of the deep root 1 (*Dro1*) gene [187] has been utilized for improving drought tolerance [303]. Similar strategies with homologs of deep root genes are being explored for other cereals such as wheat [350]. The utility of *Dro1* homologs in the improvement of salt tolerance in rice has been demonstrated [351].

The physiological and molecular responses of rice to flooding have been extensively studied [315], providing evidence for several traits associated with submergence tolerance. The most progress was the discovery and deployment of the SUBMERGENCE 1 (*SUB1*) locus in rice, conferring tolerance to complete inundation (submergence) [308,352]. *SUB1A* was identified and cloned from a submergence-tolerant cultivar, i.e., FR13A, and it had been developed through selection from farmers' variety "Dhallaputia" grown in Odisha (India). *SUB1A* is the dominant gene(s), and fine mapping of this gene on chromosome 9 has been completed. A marker-assisted backcross breeding approach is now being successfully exploited for the development of high-yielding submergence-tolerant rice cultivars. Under mild stress (5–6 days submergence), plant mortality in rice is generally very low, yet extensive leaf damage occurs. However, the damage is almost nil in cultivars with *SUB1* QTL genes due to the maintenance of higher activities of antioxidant enzymes. Prolonged water stagnation decreases the grain yield in cultivars with *SUB1* (*Swarna-Sub1*) compared to those without *SUB1* (e.g., *Swarna*). Sarkar et al. [353] suggested that *Swarna-Sub1* is suitable for flash flood conditions. They also concluded that the maintenance of chloroplast integrity could be a better option for predicting the plant survival under submergence. Some researchers believe that the ideal combination for an adaptation to complete flooding is submergence tolerance (survival underwater) together with some elongating abilities [353].

The geographical distribution of these accessions harboring *SUB1A-1* suggests that *SUB1A-1* from wild species might have introgressed around the Ganges Basin and subsequently spread to other areas of South Asia [354]. By contrast, *SUB1A-1* is absent in submergence-tolerant accessions of wild rice with the CC genome (*O. rhizomatic* and *O. eichingeri*) and the CCDD genome (*O. grandiglumis*) [355,356], suggesting the presence of a *SUB1A*-independent mechanism in these rice species. Future elucidation of the *SUB1A*-independent mechanism may contribute to the future breeding of cultivated rice with strong flash flood tolerance.

A recent significant discovery of the cloning of the Leaf Gas Film 1 (*LGF1*), a wax synthesis gene involved in the leaf hydrophobicity and formation of the gas films necessary for gas exchange and underwater photosynthesis, is another important step towards developing flood-tolerant varieties [311]. There is evidence that cuticular wax accumulation is associated with drought tolerance in wheat [232], maize [357], and beans [358]. The dynamics of wax accumulation in leaves of wheat have been recently elucidated [359]. The discovery of *LGF1* briefly gave insights into the potential shoot and root traits that can improve submergence tolerance in rice. Kuroha and Ashikari [293] reviewed and discussed the recent progress in understanding the various molecular mechanisms and genetic factors regulating flooding tolerance in rice.

6. Unexplored Mechanisms and Genes Modulating Abiotic Stress Tolerance

An in-depth understanding of stress sensing, signal transduction, and the generation of the stress response are required to develop resilience to multiple abiotic stresses in grain crops, including major cereals and legumes. Uncoupling the molecular processes associated with stress tolerance is crucial for generating climate-resilient crops. It is crucial to differentiate the plant responses observed under a particular environmental stress factor and responses observed under a combination of stresses for developing climate-resilient crops [360]. Hence, there is an urgent need to include stress combinations while studying the plant responses to abiotic stress, employing molecular genetics, molecular breeding, or molecular physiology. Another challenging task is to link the biological processes at different scales [360]. The crops in silicon initiatives, wherein multi-scale models try to generate new concepts, prioritize bioengineering efforts in plant research [361]. The challenge is to build developmental models that fit well with the biological traits of the crop species and explain the plant responses to changes in the environment [360]. Multi-level models incorporating data from genetic, epigenetic, and transcriptional studies, along with data regarding splicing and post-transcriptional regulation, are likely to provide new insights into plant molecular responses under abiotic stresses [362]. The integration of machine learning algorithms with transcriptomic data and high-throughput phenotypic data is now essential to accelerate gene discovery processes, including genome annotation and gene regulatory network predictions [363].

Several traits associated with multiple abiotic stress tolerances are encoded by genes that were lost during cultivation. Large numbers of genetic resources of crops with diverse genetic variations are available; hence, there is ample scope to recover traits associated with resilience to abiotic stresses. Advances in genomics, molecular genetics, and phenomics, coupled with new methods for capturing genomic regions associated with abiotic stress tolerance, could be promising for attaining climate resilience in cereals and legume crops. The pyramiding of genes into a single background is now a viable strategy. Assembling appropriate gene combinations in elite varieties is a challenging task. Addressing the yield loss due to abiotic stress requires innovative technologies like genome editing and epigenetic modification. Combining genetic resources and transformative technologies from genome editing to synthetic biology could be helpful strategies to identify traits associated with tolerance to a multitude of abiotic stresses. Some novel opportunities are discussed in this section.

6.1. ABA Receptors

ABA is a master controller of transpiration and regulates ion channels and the expression of genes associated with abiotic stress tolerance in plants. ABA interacts synergistically or antagonistically with salicylic acid, jasmonic acid, and ethylene to regulate responses. The plasma membrane-localized G protein-coupled receptor (GPCR) and type G proteins (GTGs) [364] were considered ABA receptors. However, their targeted roles in signaling pathways and conservation in grain crop species remain characterized. The genetic manipulation of ABA signaling can be useful. The ABA signaling components, comprising of the ABAR–ABA–PP2C complex and SnRK2s, control ABA-mediated stomatal closure via ion transportation in guard cells, and there are transcriptional regulations required to develop stress responses. Further studies need to be carried out to illustrate the ABA signaling pathway components and effector genes. The PYL-ABAR gene family members differ in their tissue-specific responses, stress-responsive expressions, dimerization, and binding capacities to ABA. Hence, the physiological relevance of different combinations of ABAR–ABA–PP2C needs to be elucidated.

6.2. Engineering Orthogonal Receptors

An orthogonal receptor is an engineered receptor that can bind specifically to a synthetic ligand, which cannot interact with the natural receptor. The orthogonal receptor is not activated by the basal level of the endogenous ligand. The orthogonal receptor

is helpful since they get activated by synthetic ligands at low concentrations, while the natural receptors require relatively higher doses of synthetic ligands for activation. The orthogonal receptor can be used to design crops for resilience to multiple abiotic stresses, where synthetic agonists or antagonists can be used to induce a specific physiological process such as metabolite production and tolerance to abiotic stress [365]. These studies may be crucial to engineer and use orthogonal receptors for enhancing stress tolerance.

6.3. Novel Transcription Factors

Plants have evolved sophisticated stress response strategies and harbor genes that encode transcription factors (TFs) to regulate the expression of stress-responsive genes. TFs could be candidates for enhancing resilience to multiple abiotic stresses. Recently, the TF modulation and overexpression approaches have been employed in crop plants; however, the diversity of TFs largely remains unexplored. TF families such as NAC, MYB, WRKY, bZIP, and ERF/DREB have been successfully characterized for their roles in eliciting abiotic stress responses. About 10% of genes encode TFs, which play an important role during different stages of the plant life cycle for a specific function [366]. Therefore, elucidating the mechanisms of the actions of TFs is crucial to explore the mechanism associated with plants' responses to various abiotic stresses. There is the potential to engineer crops with TFs to enhance their tolerance to many stresses and characterize TFs for their role in stress tolerance in plants [367].

Advanced technologies like chromatin immunoprecipitation with massively parallel sequencing (CHIP-Seq) and next-generation sequencing (NGS) could be beneficial for genomic region identification for deciphering the role of TFs. The CRISPR/Cas (Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-associated protein) gene-editing tool can be used to modulate TFs. In addition, the functional redundancy of TFs needs to be addressed. Although previous analyses of TF overexpression in response to a specific stress have been very informative, studies are required to investigate whether the overexpression of stress-related TFs in transgenic plants enhances stress tolerance and growth without any yield penalty. Further studies are required to understand the mechanisms of the action of several TFs and their role in enhancing stress tolerance in food grain crops.

7. The Metabolic Control of Resilience to Abiotic Stress

The molecular breeding and molecular genetics for the genetic enhancement of plants for yield stability under adverse environmental conditions could potentially capture the effective resilience to abiotic stress. Plants generally reduce vegetative growth and accelerate reproductive development under stress. The genetic variations and underlying mechanisms that enable drought-resilient plants to conserve soil moisture and delay the accumulation of biomass until grain filling largely remains unclear. Higher yields under well-watered conditions and under a moderate drought at the time of flowering were achieved in corn that expresses a metabolic enzyme that converts trehalose-6-phosphate (T6P) to trehalose in the phloem companion cells at the base of the ear and in developing florets [368]. The modulation of T6P facilitates the photosynthate's mobilization to the unfertilized floret and prolongs the photosynthetic activity of leaves during grain filling. Thus, novel genetic variations and genetic enhancements can achieve the integration of the metabolism and stress resilience to improve crops for yield stability under adverse environmental conditions.

8. Engineering Plants for Biomass Production under Abiotic Stress Conditions

Recent advances in molecular genetics and genomics have enabled the identification of a complex signaling network associated with plant growth and development. Many genes have been identified and characterized for their role in abiotic stress tolerance, employing genomics and molecular genetics. However, efforts should be made to unravel the crosstalk between the transcriptional circuitries for biomass production and abiotic stress responses. This knowledge could serve as a valuable resource to eventually custom design the crop

plants for higher biomass production with less water use in a more sustainable manner under adverse environmental conditions.

The adaptation of plants to various abiotic stresses is a coordinated response involving many genes and their interactions with various environmental factors during the entire life span of crop plants [369,370]. Accordingly, a thorough understanding of the molecular responses in plants is crucial for improvements in plant biomass or yields. Advances in molecular genetics, genomics, tissue-specific or developmental stage-specific gene expression, and gene pyramiding can be promising in enhancing the photosynthetic efficiency in plants, contributing to a higher biomass.

Plant cell wall polymers form a significant component of plant biomass. The composition and amount of these polymers in the cell wall change with the developmental stage of plants and in response to stress conditions [371]. There is a need to delineate the genes associated with the biosynthesis of different cell wall components. In addition, manipulating endogenous plant hormones will further widen the scope of improving stress tolerance and biomass production. Integrating the key regulatory genes and transcriptional regulations of secondary cell wall biosynthesis through the cascade of activators and repressors could be crucial for designing crop plants with enhanced biomass under stress conditions.

9. Future Perspectives and Conclusions

The challenge of improving abiotic stress tolerance in crops must be addressed with an understanding of the underlying complexities and with care taken to avoid grain yield penalties resulting from the introgression of relevant traits. A feasible approach to addressing this challenge should include the grain yield and the traits specific to targeted agro-ecologies. Although the possibility of improving stress tolerance has been successfully demonstrated through transgenic approaches, breeding varieties tolerant to abiotic stress is difficult. This has been attributed to the underlying complex mechanisms that influence the relevant traits and associated genes, which often act in coordination. There is ample scope for integrating different omics strategies to increase plant stress tolerance substantially, as marker-assisted selections by employing stress-related genes and QTLs are becoming more routine activities in the crop breeding program. Advanced tools such as CRISPR/Cas techniques for the modification of genes are becoming more relevant for the genetic improvement of abiotic stress tolerance in plants.

Recent advances in omics approaches, including genomics, proteomics, and phenomics have provided new opportunities for understanding abiotic stress responses in plants at a different scale, from the cell level to the whole plant level. Designs for stress-tolerant crops can be substantially improved with the additional insights into the mechanisms of stress tolerance in plants obtained through deep sequencing technologies and other omics approaches, such as metabolomics (Figure S2). Information emerging from epigenetics can be useful in understanding the mechanisms of the stress-memory of plants. Advances in molecular breeding methods can accelerate the use of functional molecular markers in marker-assisted selection. In addition, genomic tools can assist in understanding the gene networks associated with plant stress.

The existing knowledge gaps that are hindering the application of omics for abiotic stress tolerance in crop plants must be bridged through a system biology approach. Tools and methods for high throughput phenotyping must be optimized for the identification of relevant genes and their utilization in breeding different crops. This is likely to be aided by the emerging tools for extensive data analyses, which employs machine learning algorithms. Conventional approaches to crop production are now being complemented by remote sensing tools that are integrated for crop stress monitoring. Advances in imaging and sensor technologies, high throughput phenotyping, and remote sensing tools can enable rapid field-scale estimations of plant health and plant stress susceptibility or tolerance, guiding crop management decisions under an abiotic stress environment. The systematic evaluation of extensive germplasm collections to identify tolerant genes and genotypes, and the development of targeted breeding programs to enhance abiotic stress tolerance

using traditional and novel methods, are both essential for increasing the yield and stress tolerance of food grain crops.

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